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SOME CONSIDERATIONS ON THE DISTRIBUTION OF FISHES IN ONTARIO

By

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TAXONOMIC LIST OF SPECIES

Species marked with an asterisk have not been recorded from Ontario waters.

INTRODUCTION

The geographical distribution of animals and plants both fossil and living, is a subject of considerable value in the investigation of the climatic and geological history of the earth. Distributional studies have also formed the basis upon which the earth has been divided into convenient systems of geographical zones. A knowledge of the distribution of different taxonomic units leads to a better conception of their relationships, thus providing evidence for the effect and importance of isolation, hybridization and mutation, and, in this way, contributes to a great extent to the understanding of the principle of evolution.

The extent of the area occupied by living forms is the resultant of two primary forces—geological and ecological, acting individually or in conjunction with one another, one sometimes assisting the other towards its goal, sometimes working in an opposing direction. Barriers raised by one factor are frequently capable of counteracting the distributional channels offered by the other. The relationship of the distribution of fishes in Ontario to the factors mentioned forms a significant illustration of the complications underlying distributional problems. To describe distribution is one matter, to explain it, something very different. This paper is an attempt to describe the distribution of Ontario fishes and to offer feasible explanations for their dispersal.

The present distribution of the flora and fauna of Ontario has developed within the last 20,000 to 35,000 years, (Coleman, 1922—p. 68), the time estimated to have elapsed since the beginning of the last ice retreat in eastern North America. Before that time all of Ontario lay beneath a vast glacier and any living organisms which had inhabited the area before the onset of the glaciation were forced to withdraw into areas not affected by it, or were exterminated. When the ice sheet began its last retreat in a general northerly direction, new land areas and new waterways were made available. These were populated, in the course of time by plants and animals, due to the natural tendency of species to spread into every available habitat.

Before proceeding with the actual facts of distribution of fishes in Ontario it will perhaps be well to look into the geographical history of the area under consideration.

Geological History of the Principal Drainage Systems of Ontario

EARLY HISTORY OF GREAT LAKES REGION.

In early Palaeozoic times, a shallow sea stood over the present Great Lakes region and deposited sediments along the edge of the

Canadian shield which formed its northern shore. At some time during the late Palaeozoic the area bordering the old Precambrian continent began to rise until finally it stood above the sea as a plain sloping to the southwest.

In the long ages which followed, erosive forces attacked the sedimentary rocks overlying the granite of the Canadian shield and stripped them off for a long distance south of the old shore. This gradual eating back of the sedimentary rocks by "differential weathering" was responsible for the development of the Niagara escarpment.

It is believed that before the beginning of the glacial period the Great Lakes region stood much higher above the sea than it does at present, resulting in a steepening of the grade of drainage. There were probably no large lakes—all waters, being rapidly carried off by rivers.

The main drainage system, according to Spencer (1907) whose views in this respect seem the most probable, consisted of the Laurentian River, fed, in the main, by tributaries from those watersheds and basins now occupied by the Great Lakes. This great river flowed on or near the edge of the old continent and reached the ocean in Cabot Strait between Newfoundland and Nova Scotia. The course of the Laurentian River (fig. 1) as described by Spencer, extended northeastward from the deeper part of the Lake Michigan basin to Lake Huron, southeast to a point opposite Bruce Peninsula where it was joined by the Huronian River from the Saginaw Bay area and a branch from the southern end of Lake Huron. Then turning northward it skirted Bruce Peninsula to Georgian Bay, passed southeast along the escarpment to Barrie and southward past Toronto to the Lake Ontario basin where it was joined by the small Dundas branch with the larger Erigan River which drained the basin of Lake Erie. Continuing almost due east the Laurentian River received two smaller streams from New York State before continuing on its way to the sea. It is uncertain whether the whole of the present St. Lawrence Valley was used by this river, since there are indications that an outlet southeast of the Thousand Islands carried the channel by a more southerly route to the St. Lawrence valley at Lake St. Francis from which point the present river valley was occupied until the Cabot Strait channel to the sea was reached.

The basin of Lake Superior is not included in Spencer's river system. It is not certain whether the preglacial basin of that lake drained into the Mississippi Valley or into the Laurentian system at the head of Lake Huron. There are also indications of southward outlets to the Mississippi from the Lake Michigan and Erie basins. At present it is impossible to decide which outlet was the true one and it may be suggested that perhaps both Laurentian and Mississippi outlets may have been active in pre-glacial times. In any event the above outline

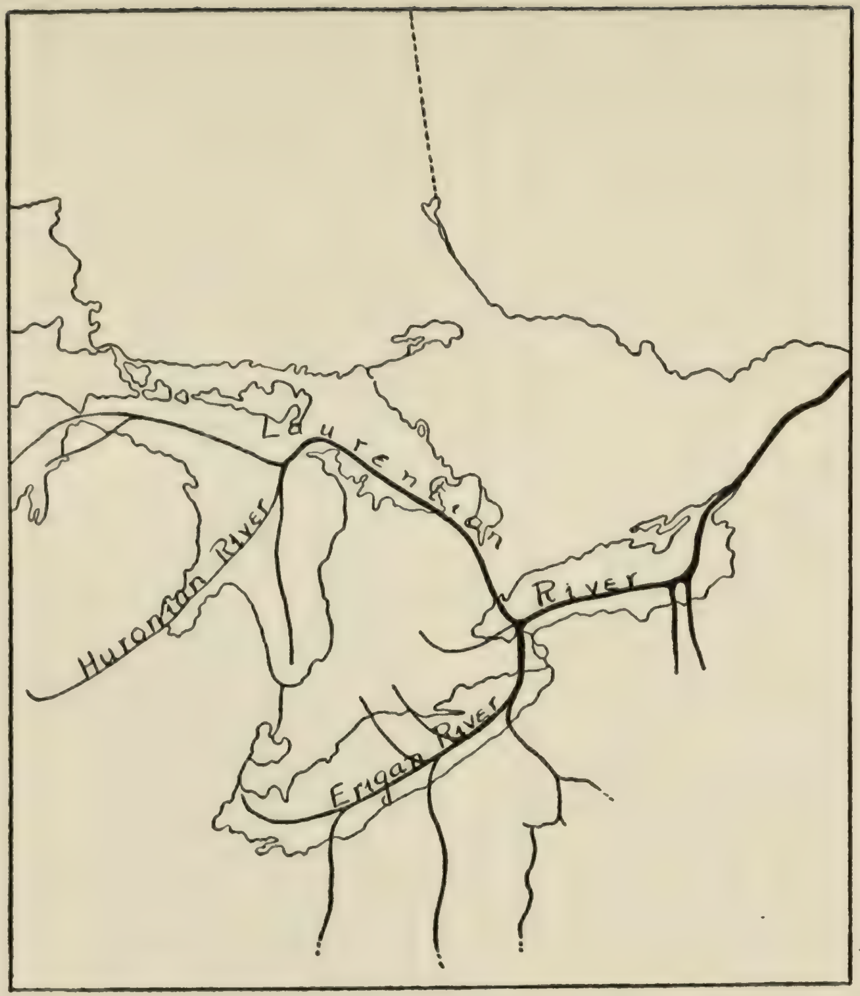


Figure 1. The course of the Laurentian River (after Coleman, 1922).

Figure 2. The extent of the Pleistocene glaciation in North America (after Chamberlin and Salisbury, 1906).

will serve to indicate the original status of the basins of the Great Lakes before the onset of the last glacial period, and this to assist in explaining the development of the glacial lakes and their successors.

THE LAST GLACIAL AGE IN NORTH AMERICA.

The several theories of the cause of the change in climate which brought on the last glacial period need not be discussed here. During the Pleistocene or Glacial period the effects of the increasing severity of climate began to appear in the more widespread occurrence of glaciers. In North America the glaciation spread from three main centres, giving rise to the Cordilleran, Keewatin and Labrador ice sheets whose relationship and maximum extent are illustrated in fig. 2. Most of the northern half of the North American continent was covered by this vast ice mass, although most of Alaska, part of the Yukon and a large area in Wisconsin show no evidence of glacial drift and are believed to have been left exposed during the Pleistocene glaciation.

According to Chamberlin and Salisbury (1906, page 420) the time since the last ice invasion is estimated to be from 20,000 to 60,000 years as compared with Coleman's estimation of 200,000 to 35,000. The duration of the whole glacial stage including all its phases of retreat and advance has been estimated by Chamberlin and Salisbury (1906, page 420) as approximately one million years.

During the Pleistocene glaciation there were intervals when the climate became milder, and the ice retreated and readvanced several times over its southern regions. Five of these ice invasions are indicated in Iowa. In Canada there is evidence of at least two retreats in which the basin of Lake Ontario was free from ice. It is quite likely that the basins thus freed were occupied by lakes much like the present Great Lakes, but these have little bearing on our problem and we shall proceed to a discussion of the more significant lakes which developed with the final retreat of the ice.

Whatever had been the cause of the change in climate must have ceased to be effective, for the climate gradually became milder and the glaciers began to melt away at their southern borders. The last recession of the Pleistocene ice cap had begun. Due to the numerous valleys underlying the glacier, which were gradually exposed as the ice withdrew, the borders of the glacial sheets assumed a lobulate form in their retreat as they had in their advance, with lobes extending into the depressions between ridges.

LAKE AGASSIZ.

It has usually been considered that this body of water which formed in the Lake Winnipeg area occurred earlier than the other glacial waters

for which the retreating glacial sheets were responsible. The impression appeared to be that the Cordilleran sheet began its withdrawal earliest, followed by the Keewatin and later by the Labrador. At present the relative time of the occurrence is uncertain. However that may be, it is recognized by all that the water produced by the melting of the lower portions of the Keewatin lobe were ponded in the Red River valley, and since all possible northern outlets were closed by the remaining portion of the Keewatin sheet flanked by the Labrador sheet to the east, the rising waters in the valley were forced to find an outlet to the south into the Mississippi Valley, through what has been termed the Warren River into the Minnesota River, a tributary of the Mississippi. Lake Agassiz was comparatively shallow and at its maximum extent covered an area of 110,000 square miles, occupying parts of Saskatchewan, Manitoba, Ontario, Minnesota and North Dakota (fig. 3). The retreating ice sheet finally separated, opening a channel to the northeast, the origin of the Nelson River. This drained Lake Agassiz to such an extent that the Mississippi outlet disappeared and the vast lake was succeeded by a series of smaller bodies of water, Lake of the Woods, Lake Winnipeg and many lesser lakes.

The fauna of Lake Agassiz was much the same as in Lake Winnipeg at present (Coleman 1922, p. 17). In spite of the presence of northern and eastern shores of ice, it is easy to understand that the southern waters of this large shallow lake would be warmed considerably in summer, which would allow species whose range extended far into the warm waters of the lower Mississippi to penetrate into this area. It thus becomes a comparatively simple matter to account for the repopulating of the waters of the Lake Winnipeg and Lake of the Woods area.

THE GLACIO-LACUSTRINE SUBSTAGE IN THE GREAT LAKES AREA.

As the Labrador ice sheet retreated towards the northeast the basins previously drained by the Laurentian River began to be exposed. The water resulting from the melting ice was ponded first in small depressions giving rise to numerous small lakes draining to the south and southwest by innumerable streams through every available pass in the divide into the Mississippi Valley. As time went on more and more of the present lake basins became exposed, the lakes increased in size, the ponded waters tended to unite along the edge of the retreating ice and to utilize only the lowest outlets across the divide. This process lowered the lake levels to such an extent that when the ice withdrew so far as to permit still lower outlets to the southeast and finally to the northeast through the St. Lawrence valley, the lake levels fell still lower on the Great Lakes side of the divide separating them from the Mississippi, and the

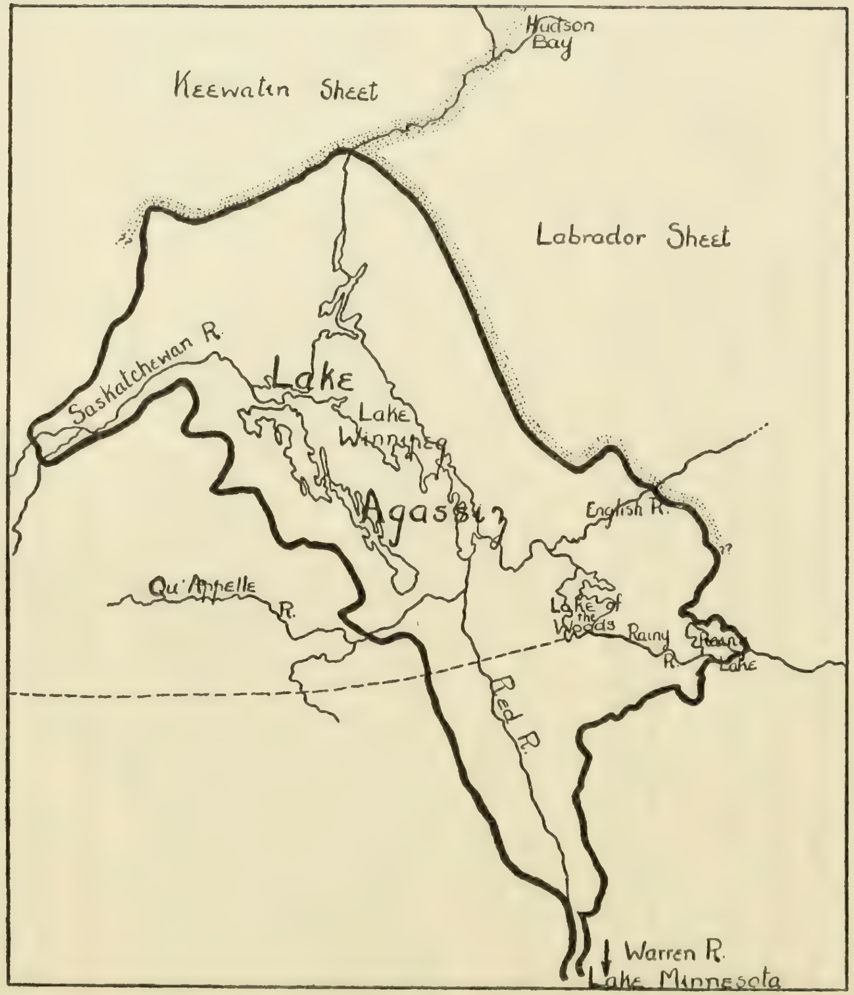


Figure 3. Lake Agassiz (after Upham, 1895).

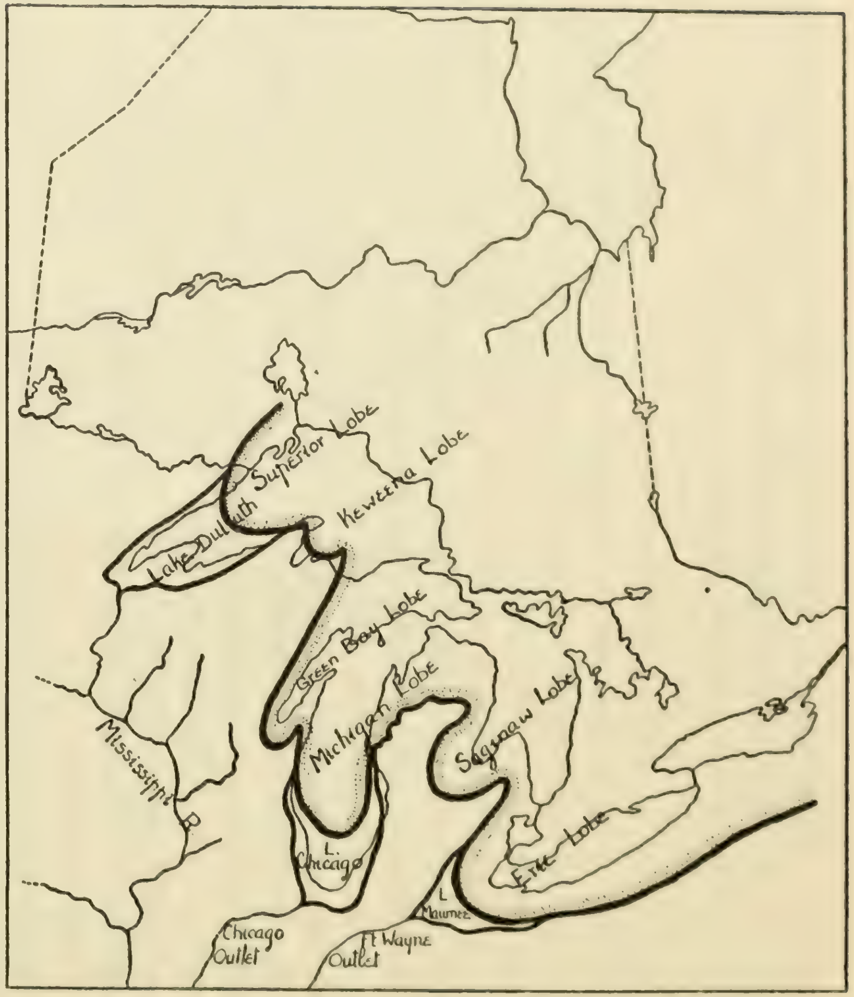


Figure 4. The earliest postglacial precursors of the Great Lakes (after Taylor and Leverett, 1910).

outlets across this divide were abandoned resulting in the present rock bound lakes in place of the earlier ice-ponded stages.

In the Lake Superior region a crescentic lake (Lake Duluth, fig. 4) formed about the head of the retreating Superior lobe in the southwest part of the basin, and discharged over the divide to the Mississippi through a channel at the head waters of the Brule and St. Croix rivers in Minnesota. Similar crescentic lakes formed about the withdrawing Michigan and Erie lobes in the basins occupied by these lakes. Lake Chicago, the glacial lake formed at the foot of Lake Michigan discharged into the Illinois valley through an outlet southwest of Chicago. The valley left by this outlet has since become the site of the Chicago drainage canal. The lake which appeared at the end of the Erie ice-lobe has been termed Lake Maumee, draining by way of Fort Wayne into the Wabash and thence to the Mississippi. The positions of these lakes and their outlets are indicated in figure 4.

With the retreat of the Lake Erie lobe and consequent expansion of Lake Maumee to the north and east along the borders of the lobe an outlet to Lake Chicago which was expanding northward was found along the edge of the Saginaw lobe and at a lower level than the Fort Wayne outlet. In this second stage of Lake Maumee the waters drained westward across the Michigan peninsula from Imlay into the Grand River valley and thence to Lake Chicago (fig. 5). Later a retreat of the Saginaw lobe produced a Lake Saginaw which also discharged into the Grand River. This whole system, Lake Maumee, Lake Saginaw and Lake Chicago then drained into the Mississippi through the Illinois valley. With subsequent retreat of the ice a lower outlet from Lake Maumee was opened north of the Imlay outlet into Lake Chicago and the Grand-Imlay channel was abandoned.

Somewhat later Lake Maumee was replaced by Lake Arkona, a lake twice as large as Lake Erie. A readvance of the ice closed the northern outlet, raised the level of the water and forced it to seek an outlet to the Grand River and Lake Chicago at Ubly. At this stage the lake is known as Lake Whittlesey (fig. 6).

Further withdrawal of the Saginaw lobe resulted in a confluent ponding of the waters of Lake Saginaw and the waters in the Erie basin. The latter had meanwhile become extended into the Ontario basin where the ice lobe still blocked the eastward outlet. At first this Lake Warren stage (fig. 7) discharged through the Ubly-Grand River and Fort Wayne outlets. But with continued retreat of the ice Lake Warren crept along the glacier in the southern edge of the Ontario basin into the Finger Lake region of New York. There is some indication that an outlet to the Atlantic was opened in this region. The evidence is more convincing for an outlet farther east where the extending arm of Lake

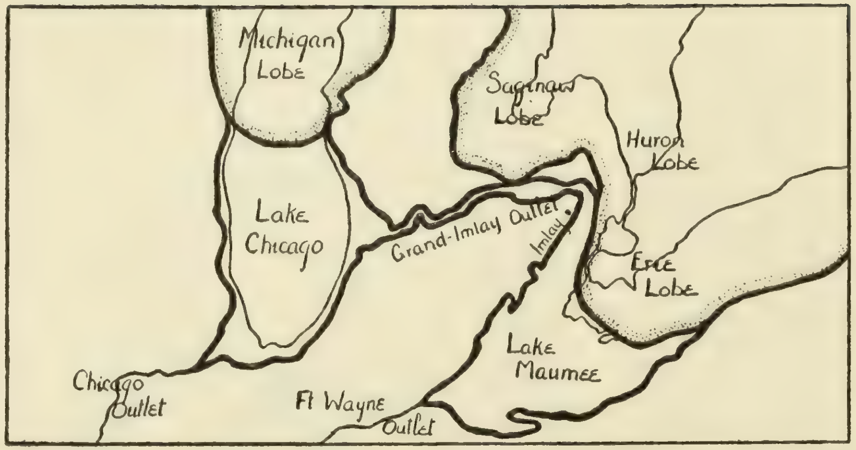


Figure 5. The Grand-Imlay connection of Lakes Chicago and Maumee (after Leverett and Taylor, 1915).

Figure 7. The Lake Warren stage (after Taylor and Leverett, 1910.)

Figure 6. The Lake Whittlesey stage (after Leverett and Taylor, 1915).

Figure 8. The Lundy stage (after Leverett and Taylor, 1915).

Warren reached a lower outlet in the Mohawk valley in the vicinity of Rome, New York and flowed through the Hudson valley to the Atlantic Ocean.

There were three successive stages of the period in which the Mohawk-Hudson outlet was in use—Lake Dana, Lake Lundy (fig. 8), and Lake Iroquois (fig. 9). The escape of the water through the lower eastern outlet reduced the level of the lake so that the Ubly outlet to the Mississippi was no longer used. Throughout the Lake Warren, Dana and Lundy stages the water in the Erie and Ontario basins was confluent and the escarpment lay well below the surface. It may be well to note here that the Fort Wayne outlet to the Mississippi Valley remained in existence throughout the changes occurring in the levels of the water in the Erie basin until the close of the Lake Lundy stage. Erosion lowered the Mohawk outlet, and the water level of the lake fell to such an extent that the escarpment rose above the surface and the waters from the Lake Erie basin spilled over the falls thus made into Lake Iroquois which came into existence in the Ontario basin. In its initial stages, when the escarpment first separated the waters of the Erie and Ontario basins and Niagara Falls appeared, Lake Iroquois existed as a small strip along the southern and western borders of the Ontario lobe, draining as stated above, past Rome into the Mohawk and Hudson valley. When the whole of the Ontario basin had been set free the lake occupied an area somewhat larger than the present Lake Ontario.

LAKE ALGONQUIN.

While the lower lakes were passing through the stages outlined above the ice continued to retreat from the basins of the upper Great Lakes. At the time when Niagara Falls and Lake Iroquois came into being, the upper lake basins were almost completely free from ice. The waters of what had originally been Lake Duluth, Lake Chicago and the expansion of Lake Saginaw into the Huron basin became confluent, with all outlets to the north and northeast still blocked by ice. Spencer has called this body of water Lake Algonquin and probably for a time the Chicago-Illinois outlet continued to drain it into the Mississippi Valley, although at the same time the Lake Erie passage to the Ontario basin was open. It is likely that both these channels operated for a time until the ice withdrew from the Georgian Bay region sufficiently to open a lower outlet past Kirkfield into the Trent valley and thus to Lake Iroquois. The great weight of ice over the land at this time caused the Trent valley region to stand at a lower level so that the draining of Lake Algonquin through this channel must have lowered the lake level considerably leaving the Chicago and Lake St. Clair outlets dry. Further retreat of the ice removed the pressure and the land was able to rise,

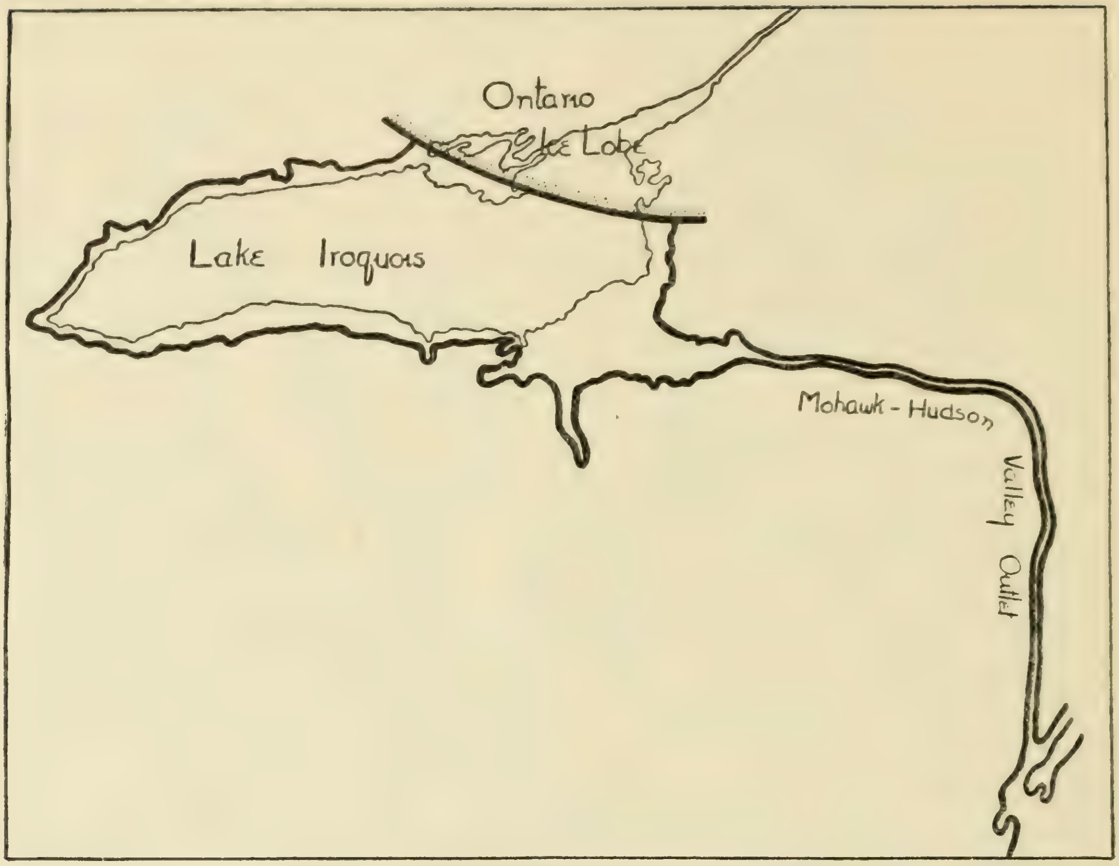


Figure 9. Lake Iroquois and the Mohawk-Hudson Valley outlet (after Coleman, 1922).

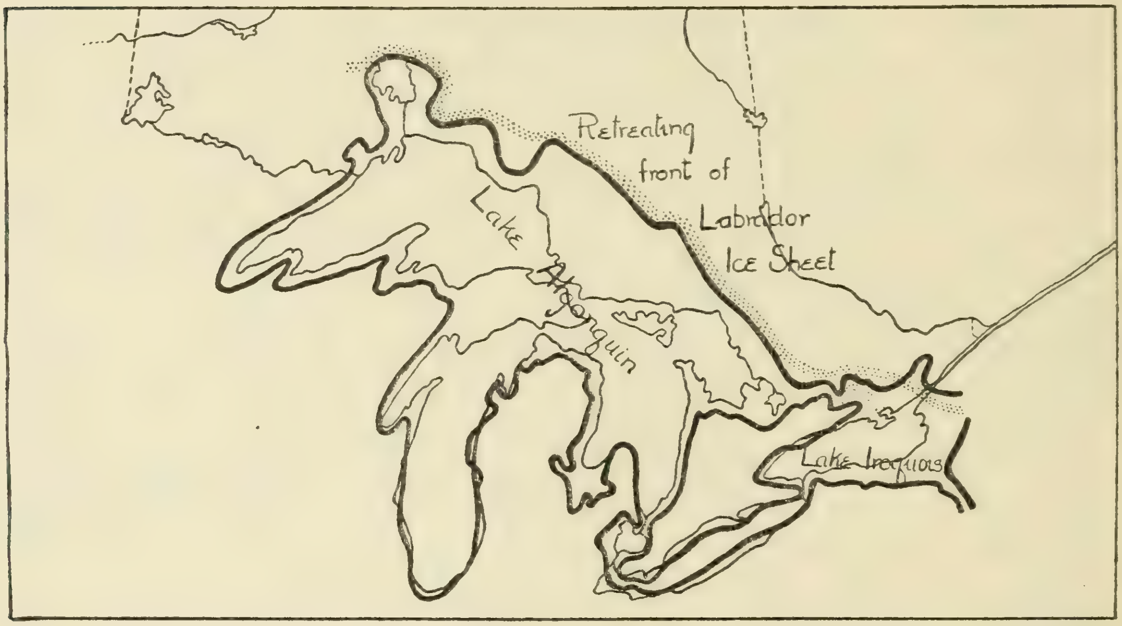


Figure 10. The Lake Algonquin stage (after Coleman, 1922).

the Kirkfield outlet was raised until the correspondingly higher level of Lake Algonquin brought the St. Clair and possibly the Chicago outlets once more into service. Eventually the elevation of the land to the northeast closed the Kirkfield or Trent outlet. The increase in the amount of water forced to escape elsewhere cut a deeper bed in the St. Clair River so that the Chicago outlet whose deepening was prevented by a sill of rock, ran dry, causing all the Lake Algonquin drainage to pass into Lake Erie.

During the two- or three-outlet stage the process of ice retreat with its subsequent land elevation seems to have undergone a long halt. On examining the map (fig. 10) it will be seen that while the southern shores of the lake basins of the Algonquin waters differed little from their present position, to the north the lake extended far beyond its present limits. A bay extending northward in the Lake Superior region included the basin of Lake Nipigon. Northeast of Sault Ste. Marie the beaches representing the old shores of Lake Algonquin stand 100 miles inland. Lake Algonquin covered some 100,000 square miles when at its greatest dimensions.

The Kirkfield outlet, or Algonquin River as it is called, probably functioned longer during the Algonquin Great Lakes stage than any other outlet. The St. Clair outlet came back into use only in the later part of the period.

The Algonquin river flowed, in the main, through the present channels occupied by the Trent valley Canal. A bay of Lake Algonquin extended over the regions of Lakes Couchiching and Simcoe and east to Fenelon Falls where the water entered the river and flowed through the basins of the Kawartha Lakes following the channel of either the Otonabee or the Indian River to Rice Lake which lay in a bay of Lake Iroquois. The Algonquin River was in existence while the Mohawk valley outlet of Lake Iroquois was still active and even after the level of the water in Lake Iroquois dropped to the Ontario level. The old Algonquin River channel, far too wide and deep to be the result of work of the Trent River, has been traced down the Trent valley to the Bay of Quinte and Lake Ontario. The fact that this channel can be traced below the present level of Lake Ontario is probably explained by the fact that when Lake Iroquois was drained the sea stood at a much lower level than at present since a much greater amount of water was bound up in the ice sheets. Lake Iroquois was thus drained until the water level stood somewhat below that of the present lake and the channel of the Algonquin River was extended correspondingly. It was just after this stage that the marine invasion known as the Champlain Sea took place.

THE NIPISSING GREAT LAKES.

The ice continued to retreat to the northeast. On its final removal from the Algonquin basin an outlet was opened through the Lake Nipissing region down the Mattawa valley to that of the Ottawa. Due to the great weight of ice still remaining to the northeast this outlet stood at a lower level than the St. Clair channel and the waters of the upper Great Lakes were lowered to a stage which has been termed the Nipissing Great Lakes (fig. 11). By this time Lake Nipigon had been separated off as a distinct lake, the lowering of the waters in the Superior basin having permitted the Nipigon River with its rapids and falls to come into existence. The shores in the Superior, Huron and Michigan basins were, in general, only slightly higher than at present but the level of the water was sufficiently high to maintain the confluent condition of the three basins. An arm from the Georgian Bay region included the valley of Lake Nipissing, as far east as North Bay, in the Nipissing Great Lakes. From this point the outlet river flowed eastward to the Ottawa valley.

The Nipissing Great Lakes existed over a long period. In the early stages while the Nipissing outlet was kept low by the weight of the ice, the water level in the lakes fell below the St. Clair outlet. The whole of the drainage of the Nipissing Great Lakes was, for a time, into the Ottawa valley. As the ice continued to retreat the land rose gradually restoring the use of the St. Clair outlet, and for the greater part of their existence the Nipissing Great Lakes made use of both outlets. In the later stages the continued rise of the land cut off the Mattawa outlet. All drainage was turned toward the St. Clair outlet and the present lakes took the place of the Nipissing Great Lakes.

LAKE OJIBWAY.

Across the divide which separates the Hudson Bay watershed from that of the Great Lakes, there are at least three passes which are very much lower than the early highest levels of Lake Algonquin. These passes are at Paint River, northeast of Lake Nipigon, Long Lake, 22 miles north of Lake Superior, and Missinaibi, 45 miles northeast of Michipicotin Bay. While the ice front still remained in these areas the penetration of Lake Algonquin beyond the divide was impossible. But as the ice retreated, the rise of the land was not rapid enough to prevent the extension of bays of Lake Algonquin across the lower parts of the divide. The bays lasted only a short time. The rise of the land to the north as the ice withdrew, raised the passes above the level of Lake Algonquin and isolated the former bays beyond the divide. It is likely that they gave rise to small lakes until, augmented by water from the

Figure 11. The Nipissing Great Lakes
(after Coleman, 1922).

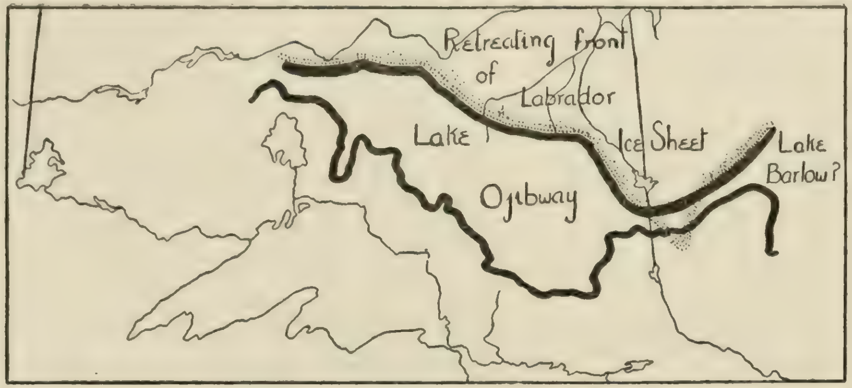


Figure 12. The Lake Ojibway stage
(after Coleman, 1922).

Figure 13. Admiralty Lake and an early stage in the marine invasion (after Coleman, 1922).

Figure 14. The maximum marine invasion
(after Coleman, 1922).

melting glaciers, they united to form Lake Ojibway (fig. 12) along the ice front. The vast clay belt extending across northern Ontario and into Quebec is ample evidence of the existence of a large body of fresh water.

Whether the whole clay belt was formed by a single lake is not yet certain. Mr. E. Wilson (Coleman, 1922, p. 42) suggests the occurrence of two lakes, Lake Ojibway in Ontario and Lake Barlow in Quebec, separated by a lobe of ice extending southward into the Temiskaming valley. The general impression seems to be that this lobe eventually withdrew so that the lakes became confluent, thus giving rise to the continuous clay belt. The western limit of Lake Ojibway is, as yet, undetermined. The clay belt extends beyond the region to the north of Lake Nipigon, but just how far beyond is not known.

While the ice sheet still remained as its northern boundary Lake Ojibway could have had no outlet to the north. Although no actual position of a southern outlet has been established, the most logical point at which this might have occurred is near the eastern boundary of Ontario. Here, the valley of Lake Temiskaming lies in the lowest part of the southern edge of the clay belt. It has been suggested that Lake Ojibway drained through a passage in the divide into Lake Temiskaming and then to the Ottawa River. If it is true that a lobe of ice filled the Temiskaming valley, as suggested by Wilson, the waters of Lake Ojibway may have flowed southward along the edge of the ice or even across it, in which case no evidence of the water channel would remain.

Eventually the retreating ice to the north of Lake Ojibway withdrew far enough to allow the water to escape into Hudson Bay. Fairly rapid draining through this outlet brought the short existence of the lake to a close. The lakes existing at present in the area, Lake Abitibi and smaller bodies of water, are regarded as remnants of Lake Ojibway and their fauna can have been derived only from the species which occurred in that lake.

LATER DEVELOPMENTS IN THE ONTARIO BASIN.

The Ontario ice lobe had not completely withdrawn from the basin of Lake Ontario when Lake Algonquin was at the peak of its development. It finally retreated sufficiently to open new, lower outlets of Lake Iroquois farther east between the ice and the northern base of the Adirondack Mountains. A series of lowerings of the water in the Ontario basin followed. At first the outlet seems to have carried the water from the Ontario basin to the north of the Adirondacks into glacial lake Champlain where it was ponded against the ice sheet and emptied into the Hudson River. One of the early stages in the Lake Ontario basin after the waters of Lake Iroquois began to recede has been termed Lake Frontenac.

With the removal of ice from the St. Lawrence Valley an arm of the sea began to extend inland through the valley, the northeastern part of the continent being depressed by the weight of the ice to the north. Meanwhile the ice had been completely removed from the Ontario basin, opening its last and lowest outlet through the present St. Lawrence Valley, so that the waters flowed out to meet the incoming marine bay. The depression of the northeastern part of the continent resulted in the draining off of much of the water from the former Lake Iroquois. The Lake Champlain-Hudson outlet dried up and the water in the Lake Ontario basin fell to a much lower level than at present. This stage has been called Admiralty Lake (fig. 13) and into this body of water the Algonquin River drained the Algonquin Great Lakes, cutting the Trent Valley channel deeper and wider and extending it beyond the region of the shores of present Lake Ontario. The early marine stage at this time filled the St. Lawrence Valley as far inland as Prescott, Ontario, where the outlet of Admiralty Lake had its mouth. This marine bay covered most of Ontario south and east of Ottawa.

It was at this time that the northeastward rise of the land removed the Algonquin River from its level of usefulness. The St. Clair River became for a time the sole outlet for the upper lakes. Shortly afterwards the Nipissing Great Lakes came into existence as previously outlined. Then also, Lake Ojibway developed to the north of the divide. The marine invasion through the valley of the St. Lawrence reached its maximum extent (fig. 14) encroaching even into the Ontario basin, as the Gilbert Gulf, extending northwestward across the eastern tip of Ontario to meet the Mattawa outlet of the Nipissing Great Lakes in the Ottawa valley (fig. 11). A bay of this marine arm filled the Lake Champlain basin and was probably connected southward by a narrow strait along the Hudson Valley to the ocean.

Dawson (Coleman, 1922, p. 57) held that a marine invasion extended from the Hudson Bay region across a lowered portion of the divide to meet the northward extension of the Champlain Sea. It seems quite true that a marine stage did occur after Lake Ojibway on the Hudson slope but its most southerly point is unknown. Hudson and James Bay certainly extended much farther inland than they do at present, which is explained by the fact that the land had not recovered from its depression under the load of ice. On the southern slope of the divide the maximum marine invasion extended a long fjord up the Temiskaming valley. However this may be, there is evidence that the southern slope was the first to be unloaded and had already risen considerably before the northern slope was set free, the southern invasion which must have occurred before the land level rose very much, probably was concluded before the northern invasion began. The marine stage on the Hudson

slope is concluded to have occurred after the maximum Champlain Sea invasion, but at a time contemporary with the two outlet stages of the Nipissing Great Lakes.

Late in the period of existence of the Nipissing Great Lakes the Champlain Sea began its retreat, the submerged areas in eastern Ontario and Quebec rose above the waters and the present condition of Lake Ontario was developed. The same northeasterly rise of land which kept the Lake Ontario waters from draining to the low level of former Admiralty Lake by elevation of the Thousand Island outlet, closed the Mattawa outlet and the upper Great Lakes assumed their present boundaries.

THE ECOLOGICAL ASPECT

Although the retreat of the glacier may be regarded as the major factor in the development of the basins of the Great Lakes and other Ontario watersheds, and in opening various channels through which the redistribution of aquatic animals and plants took place, the effect of subsequent factors on the distribution of fishes must not be overlooked. The physiographic changes in the areas exposed by the retreating ice have had a decisive influence in the production of habitats, and hence in the associations of living forms which became a part of them.

As we have seen, the earliest post-glacial waters were those formed by the melting edge of the ice sheet when the glacier finally began to retreat as a result of the moderating climate. In some regions where the slope of the land was sufficient, these waters appear to have drained away as soon as formed. In others, the water remained ponded against the glacier, until, by the addition of more water from melting ice or rain, the water level was raised sufficiently to break through the barrier and drain away southward. Further retreat of the glacier increased the extent of the ponded waters and opened up new drainage areas leading into and away from these basins. Modifications of these watersheds and basins resulted when the land began to rise as the great weight of ice was removed from its surface. The changes in the watersheds were due chiefly to the "base-leveling" effect of streams, cutting back into the exposed land surfaces and carrying silt, sand and gravel downstream to be deposited in lowland areas.

Living organisms characteristically tend to expand their range into all available habitats where suitable conditions exist and where they are able to find a foothold. As soon as the streams began to flow away from the face of the glacier and from the ponded waters, establishing connections with the drainage areas to the south, water channels were available for northward dispersal and new areas opened up for repopu-

lation. The result was a great variety of habitats which were subject to change as time went on.

The work of investigators such as Forbes (1914), Shelford (1911) and Gersbacher (1937) in observing the habitat requirements of species of fishes in relation to the stages in development of streams and ponds has given us certain facts concerning ecological succession through which we may picture with reasonable certainty the path of development of aquatic habitats in the newly opened areas.

The fundamental principle underlying this development is a natural cycle through which organic debris from the surface of the earth is carried by streams to be deposited on the lake bottoms and river beds where it becomes "an aquatic soil, partly muddy water and partly wet mud, more fertile even than the richest fields and sustaining a new population of plants and animals, of many grades and classes, one climbing upward, as we may say, upon the shoulders of another to reach a level which makes them accessible again to our use" (Forbes, 1914). The fundamental factor in this cycle is food. Before an organism can become an inhabitant of any area its food supply must be available in that area. In this it is necessary to take into account the competition between different species and different types of organisms for the same food source and hence for a particular niche in the community.

Gersbacher (1937) investigated the development of communities in new pool regions formed in streams behind dams. When a dam is built, detritus at once begins to collect on the bottom of the pool so formed since the current of the stream is arrested at this point. Pool conditions are more favourable to plankton production than running water conditions and this source of food soon becomes abundant. The accumulation of dead plants which have become established in the pool region, provides a bottom layer of organic debris in which bacteria develop, providing food for communities of larger bottom dwellers which exhibit a type of progression among themselves. *Chironomus* and *Corethra* were found to be among the earliest inhabitants while *Tubifex*, Ceratopogonidae and amphipods appear at successively later stages. The kinds of fish inhabiting such a pool depend to a large extent on the type of food available. For example the gizzard shad (*Dorosoma cepedianum*) in its early stages feeds extensively on plankton, as do many young fish, but when adult it sucks up the organic mud of the bottom. This would enable this fish to enter the pool before the communities of bottom dwelling animals became established as a food source. For the most part, however, adult fish which would be present in such a stream, feed on bottom organisms, and Gersbacher observed the advent of certain species of fish as the bottom communities changed with time.

This example will serve to illustrate the type of development which probably occurred in many parts of the new drainage systems opened by the retreat of the glacier. Not all the new habitats exhibited pool conditions, however. Lakes and other standing waters show a similar succession as do ponds with certain variations. On the other hand, running waters, depending especially on the type of land they traverse, have their own peculiarities and their own specialized inhabitants. Detritus is rarely deposited on the bed of a running stream and such as is removed from suspension catches on the rough surface of stones or in the nets of *Hydropsyche* larvae or similar structures and provides food for the flattened, clinging, immature insects which dwell among the stones. The fish which inhabit running waters are dependent either on this detritus which clings to stones as does the stone roller (*Campostoma anomalum*), or on the insect larvae and other animals hidden in the gravel, or on small fish which themselves subsist on the bottom organisms.

No less important than the succession of habitats exhibited by any one body of water or part of a body of water is the longitudinal succession in stream habitats. From its source to its mouth a stream or river offers a series of habitats each with its own peculiar conditions and communities of organisms, from the clear rapid waters of the headwater areas in the hills to the still, weed-blocked and often muddy regions of the lowland sectors. The arrangement of the type habitats varies in different streams. Rapid water conditions with their associated animal and plant forms may occur between the mouth of a stream and a stretch of lowland conditions depending on the nature of the landscape. With the effect of the baselevelling process the habitats tend to move progressively upstream, always with relatively greater extension of the lowland areas while the upland and headwater associations are carried farther back into the hills. When this cutting-back action of the stream results in the merging of two watersheds it is always the headwater organisms which are the first to cross the divide. Significant in this connection is the occurrence of the speckled trout (*Salvelinus fontinalis*) on both sides of the Appalachian Mountains and of the Rocky Mountain Whitefish (*Prosopium williamsoni*) on both sides of the Rocky Mountains.

Distribution, if considered as the occurrence of an organism in any particular place, may be regarded as the sum of all the ecological factors bound up with the life of that organism. On the other hand, distribution, if considered as the extent of range of a species or the total of occurrences in a great many places, may be looked on as the resultant of the action of geological as well as ecological factors, as stated previously and it is in this broader sense that the following discussions apply.

Sources of Information

The basis of any distributional study is the collection of data regarding the occurrence of the organism concerned in a particular area. In the case of the fishes of Ontario such information has been obtained from various sources. Most significant of these are the collection in the Royal Ontario Museum of Zoology and records from scientific papers, although questionnaires, letters and some lists of collections made by different individuals have been instrumental in adding to our knowledge. For each species these records have been plotted on large scale maps of Ontario, of which the small maps in the following pages are copies. In a few instances where the number of records for a species is small, as for some forms of extremely limited occurrence in Ontario, no duplicate maps have been prepared and a note of the Ontario records is included in the text. It must be remembered, however, that while our present information permits the construction of such maps, it is by no means complete, and although it is believed that records from southern Ontario are for the most part representative, vast areas in northern Ontario are as yet unexplored in this respect so that our knowledge of the northern ranges of many species is based on extremely limited data. In spite of this handicap the maps already present an interesting picture of the distribution of Ontario fishes and permit us to discuss with growing confidence some of the problems which have arisen.

DISTRIBUTIONAL PROBLEMS

As stated in the introduction, during the last ice age most of northern North America, including all of Ontario, lay beneath the glacier and any living organisms which had populated that area before the ice age began were forced to withdraw into areas not affected by the glaciation or were exterminated. Three regions which were not covered by the ice sheets, in Alaska and the Yukon, in the Mississippi Valley, and in the Atlantic coastal plain, may be considered as possible sources of the present species of fishes occurring in Ontario by reason of the nature of the retreat of the glacier. The Alaska-Yukon area, of course, presents far more difficulties as a possible source of distribution than the other two centres. Ontario is unique in that the fish fauna of no other province contains apparent derivatives from all three sources.

Although the "driftless area" in Wisconsin may have served as a refuge for some species, in discussing the possible post-glacial sources of present Ontario fishes the general term Mississippi Valley will be used to include this area along with that part of the river valley which lay south of the glacier. It is possible that this driftless area may have been responsible for the development of some subspecific forms.

An examination of the maps prepared has shown that the various species fall into groups depending on the nature of their occurrence in Ontario waters. The present work deals with these groups as well as with some special cases concerning individual species. Since the present known distribution of fishes in Ontario alone is insufficient to provide a solution to the problem of the source of their post-glacial redistribution, a brief note of the total range occupied has been prepared for each species concerned in the following discussions. The nomenclature used is that of Hubbs and Lagler (1941).

The terms used in referring to various regions of Ontario are those outlined by Snyder (1939). An outline map showing the principal drainage areas of the Province of Ontario is given in Fig. 15.

SPECIES OF GENERAL DISTRIBUTION IN ONTARIO

As far as is known at present, twenty-four species, comprising approximately one-sixth of the total number occurring in Ontario waters, may be included in one group as having general distribution throughout the province. That is, these forms are found in some part of all the chief watersheds. At first glance it appears possible that any or all three of the likely sources of redistribution could have been the home of these types or of their ancestors during the glacial period. A further investi-

gation of the total distribution of the species, as well as of their habitat preferences, shows that in this one group are several subsidiary groups which can best be dealt with separately.

Figure 15. Outline map showing the principal drainage areas of the Province of Ontario.

GROUP I

Fig. 16 (p. 31)

Cristivomer namaycush. Great Lake trout.

Range: Northern North America from New England and the Maritimes through the Great Lakes to Minnesota and northward, from Quebec to the Northwest Territories, British Columbia and Alaska.

Coregonus clupeaformis. Common whitefish.

Range: From northern Quebec to Nova Scotia, through the Great Lakes northwestward to Alaska (Dymond 1943). Other species of *Coregonus* are found in Europe and Asia.

Prosopium cylindraceum quadrilaterale. Round whitefish.

Range: Cold deep lakes of New England and the Great Lakes drainage, northwestward to Alaska. *Prosopium* occurs through the northern waters of Asia as far west as the Yenisei River.

Berg (1936) dealing with the synonymy of the round whitefish of North America and of Siberia asserts that, in all probability, all specimens of *Prosopium cylindraceum* (as *Coregonus cylindraceus*) from the Pacific drainage of Asia must be referred to the subspecies *quadrilaterale.*

Leucichthys spp. Lake herrings; ciscoes.

Range: Species of this genus are numerous in northern parts of Europe, Asia and North America.

The distribution of the individual species of *Leucichthys* is a special problem which is not discussed in the present work.

Catostomus catostomus. Northern sucker.

Range: Northern North America from Labrador through the Great Lakes and upper Missouri basins northwestward to Alaska, and in northeastern Siberia to the Yana (Berg, 1932); mainly in deeper waters of lakes.

Esox lucius. Pike.

Range: Northern parts of Europe, Asia and in North America from Alaska to Nebraska in the Mississippi Valley and Lake Champlain and the Potomac on the Atlantic slope; prefers clean, cool waters with sluggish current.

Lota lota maculosa. Burbot.

Range: Mainly in deep water lakes of Alaska and Canada, the upper

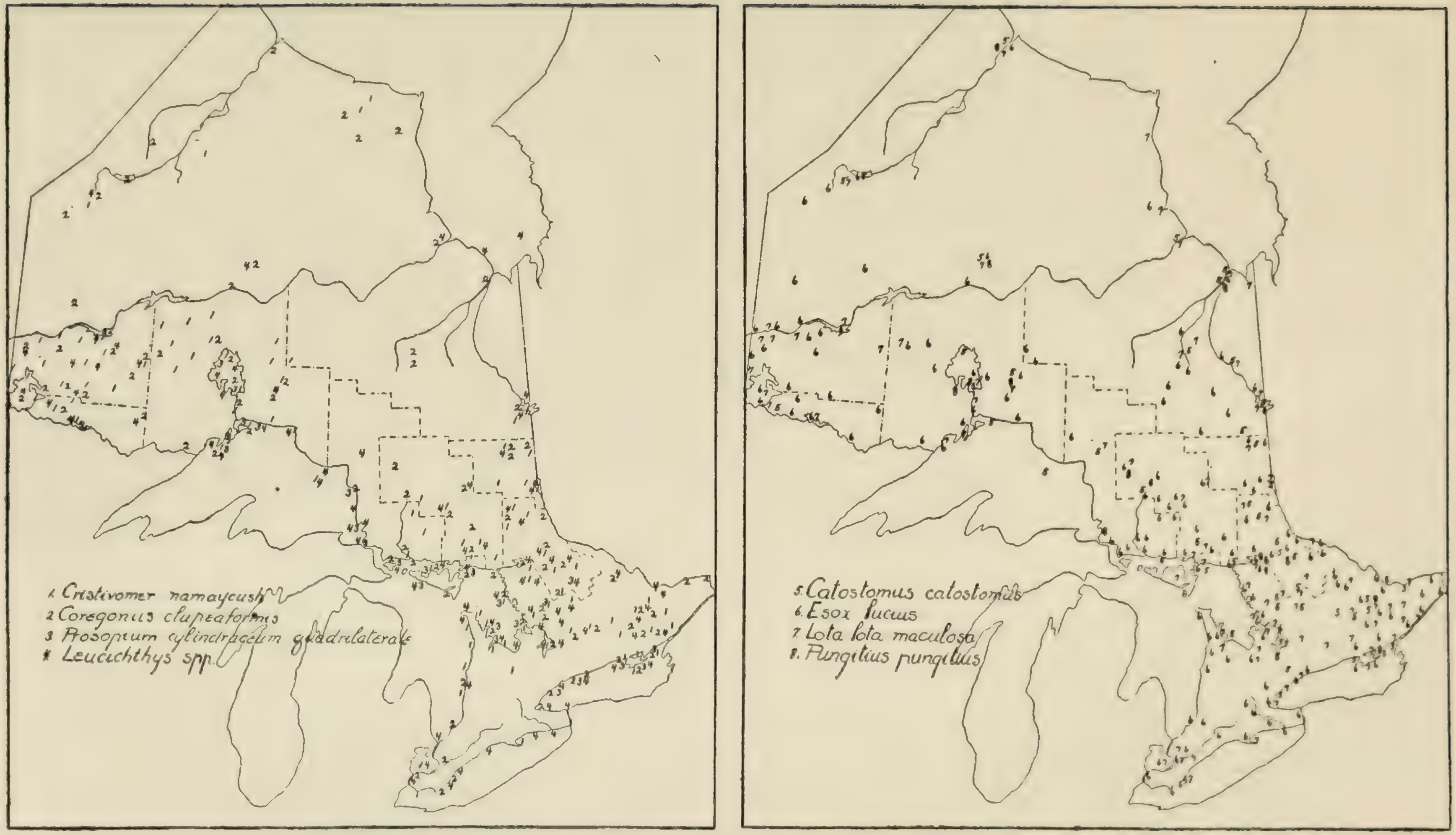


Figure 16. Distributional maps for Group I of the species which are generally distributed in Ontario.

Mississippi Valley to Missouri, eastward through the Ohio Valley and to New York. The typical subspecies occurs in northern Europe and Asia. Hubbs and Schultz (1941) regard the burbot of the Yukon River system in Alaska and Canada, and of other streams and lakes in Alaska, as separable at least subspecifically from *Lota lota lota* of Europe and most of Siberia and from *Lota maculosa* of eastern North America. To this form they have given the name of *Lota lota leptura.*

Pungitius pungitius. Nine-spine stickleback.

Range: Northern Asia, northern Europe and northern North America; cold lakes.

The distribution of the species listed above (Fig. 16) exhibits one outstanding feature. Apparently these forms range more widely through northern North America than any other Ontario fishes. The Ontario distribution of *Prosopium cylindraceum quadrilaterale* appears, at first glance, to be restricted. However, an examination of the total range of this species, as well as its habitat requirements, reveals that the need for cold, deep waters is responsible for the absence of the round whitefish from Lake Erie and much of northern and western Ontario. Had suitable conditions been available there seems to be little doubt that the Ontario occurrence of this species would have been as widespread as that of the other members of the group. Similarly in the case of *Pungitius pungitius*, habitat requirements result in its absence from Lake Erie and Lake of the Woods, although it occurs in suitable waters in all other parts of Ontario.

South and southeast of Ontario, the ranges of the members of this group are restricted. In the Atlantic coastal drainage *Esox lucius* occurs in the Hudson River, farther south than any of the other forms. In the Mississippi watershed, *Lota lota maculosa* extends farthest south to Missouri. *E. lucius* and *Catostomus catostomus* occur in the upper Mississippi Valley. *C. namaycush* is found in only the upper Mississippi drainage while *C. clupeaformis*, *P. c. quadrilaterale* and *P. pungitius* have never been reported from the Mississippi slope of the Great Lakes divide and *Leucichthys artedi* appears to be the only species of lake herring in Mississippi waters where it is restricted to the extreme upper tributaries.

Of the three possible sources of post-glacial redistribution of Ontario fishes, the Atlantic coastal region is the least likely to have been the home in glacial times of the group of fishes under discussion. Had these fishes been driven into that area by the glacier one would expect their present occurrence there to be at least moderately extensive. As it is, it is

extremely limited. And had these fishes been limited to the Atlantic coastal plain in glacial times, their redistribution would have, of necessity, taken place through the last of the post-glacial outlets at a time when some of the passages to the northwest beyond Ontario were closed, resulting in a more restricted northern distribution than these forms now have.

The possibility that some of these fishes survived the ice age in the Mississippi drainage is not so remote as in the case of the eastern area. If this did occur, then, as the glacier retreated, utilization of all the outlets would permit the fish to enter all the northern drainage basins so that the present distribution would be attained. Extension of the ranges eastward would similarly be possible. Such an explanation might suffice for the dispersal of *E. lucius*, *C. catostomus* and *L. l. maculosa* whose ability to tolerate lowland conditions to some extent might have permitted them to survive in the Mississippi Valley. In the case of the remaining five members of the group, although the waters of the Mississippi were probably kept cool by the presence of the glacier, it is doubtful whether the available habitats were entirely, if at all, suitable homes for these fish. The occurrence of fossil remains of *Cristivomer* in an interglacial clay deposit in Dunn County, Wisconsin (Hussakof, 1916) does not prove that the species survived the glaciation in this area.

At this point the need for a third source of post-glacial redistribution becomes evident. Since the present ranges of the types under consideration include Alaska and other regions where glaciers are a common feature of the landscape it does not seem unreasonable to suggest that a fish population containing representatives of these species or their ancestors was able to survive the glacial period in that part of Alaska which was surrounded by glacial sheets but not covered over as was most of northern North America (Capps, 1932). As the ice retreated northeastward, there were, in all probability, ponded waters along the ice front in the Yukon, Northwest Territories and the Western provinces. Dispersal from Alaska could thus take place along the foot of the glacier through the ponded waters to Lake Agassiz, the Hudson Bay drainage, across the divides to the Great Lakes basin, into the upper Mississippi Valley by means of the southern glacial outlets, and eastward to Quebec, New England and the Maritimes, utilizing the channels provided by Lakes Algonquin and Ojibway, the St. Lawrence system and the Hudson valley outlets. This view is strengthened by the occurrence in Eurasia of close relatives if not the identical form of all the species in this group except *C. namaycush*. Berg (1936) states "The occurrence of a North American form in northeastern Siberia is not unique among true freshwater fishes. Besides *Coregonus cylindraceus quadrilateralis*, the following species may be mentioned as having such a distribution: *Thymallus*

arcticus signifer (Richardson, 1823); *Thymallus arcticus pallasi* Valenciennes, 1848, . . . *Coregonus nasus* (Pallas); *Catostomus catostomus rostratus* (Tilesius) and *Dallia pectoralis* Bean." It is not unlikely that the unglaciated area in Alaska has contributed to the repopulation of the waters of the Eastern Hemisphere as well as of the Western.

The absence of *C. clupeaformis*, *P.c. quadrilaterale* and *P. pungitius* from the Mississippi drainage and their preference for cool lakes, deep, cold water and clear, cold streams or lakes, respectively, leads to the conclusion that the turbid lowland streams of the Mississippi plains would not provide suitable habitats for these species during the glacial period, although the waters must have been cooler than at present due to the presence of the glacier and the more severe climate. This view seems applicable also to *C. namaycush* and *Leucichthys* spp. whose occurrence in the Mississippi drainage is limited to the most northern waters. It is possible that the extreme variability known to occur among the Coregonidae has brought about the difference between the eastern and northwestern representatives of this family in the same manner that the present Great Lakes species of *Leucichthys* have become modified in the different lakes since the ancestral types entered the Great Lakes basin. It seems likely that the species of *Coregonus*, *Prosopium* and *Leucichthys* which occur in Ontario have been derived from an Alaskan centre of post-glacial distribution into which area the ancestor of the present North American coregonids was forced to retreat at the onset of the ice age. *C. namaycush* and *P. pungitius* also seem to be of Alaskan derivation. The validity of this theory of an Alaskan centre of redistribution is strengthened by the fact that the ranges of the five types believed to have been derived solely from this source are continuous from a narrow area of distribution in eastern North America towards a widespread range in the northwestern part of the continent. The other three species, *C. catostomus*, *E. lucius* and *L. l. maculosa*, whose present range includes Alaska, but which are able to withstand lowland conditions may have been derived from an Alaskan population, but there is a possibility that a Mississippi element occurred as well, and has been partially responsible for the present distribution.

GROUP II

Fig. 17 (p. 35)

Acipenser fulvescens. Lake sturgeon.

Range: Hudson Bay drainage as far north as the Churchill River in northern Manitoba, west in the Saskatchewan River to Alberta, south in the Mississippi drainage to Nebraska, Missouri and the Tennessee River of Alabama, in the basins of the Great Lakes, St. Lawrence and

Figure 17. Distributional maps for Group II of the species which are generally distributed in Ontario.

Lake Champlain; in larger rivers and lakes, ascending streams in spring to spawn.

Notropis atherinoides. Emerald shiner.

Range: From the St. Lawrence River and Lake St. Champlain south to the Potomac, westward through the Great Lakes to the Red and Saskatchewan Rivers, northward to Lake Athabaska and southward to Tennessee and Kansas; in lakes and larger rivers.

Notropis heterolepis. Black-nose shiner.

Range: From the St. Lawrence River and Lake Champlain to the Dakotas and the Assiniboine River, northward into the Hudson Bay basin and southward through Nebraska, Kansas, Arkansas and Texas; in smaller streams and lakes.

Pfrille neogaea. Fine-scale dace.

Range: From New Brunswick and New England to South Dakota, very local through the Mississippi Valley to Nebraska and northward to Hudson Bay, (Fort Severn, Dymond and Scott, 1941); boggy waters.

Pimephales promelas. Fathead minnow.

Range: From Lake Champlain, the Great Lakes and the Hudson Bay watershed to the Red and Saskatchewan Rivers; through the Ohio basin and the Mississippi southwest to the Rio Grande; in a wide variety of streams, ponds and lakes.

Stizostedion canadense. Sauger.

Range: Through the Great Lakes and parts of the Hudson Bay drainage to the Red and Assiniboine Rivers; in the Mississippi Valley west to Montana and south to Tennessee and Arkansas; in lakes and rivers.

The distribution of the six species comprising this second subgroup (fig. 17) is characterized by two outstanding features. In the first place, the fact that these species range from the Hudson Bay drainage to the lower Mississippi waters indicates a wide temperature tolerance, which supported by the present wide distribution in Ontario, leads to the assumption that these fish probably followed the retreating glacier rather closely. Secondly, one species only, *Pfrille neogaea*, occurs as far eastward as New Brunswick. The remaining species except for *Notropis atherinoides* range no farther than Lake Champlain or the upper St. Lawrence basin. On the other hand, representatives of these types

occur widely through the Mississippi Valley. Because these fish form such a well-established part of the present Mississippi fauna, and not of that of the Atlantic coastal region, we may reasonably conclude that the members of these species now inhabiting Ontario waters, as well as those in areas east of Ontario, have been derived from the Mississippi population. In their migration to the north as the glacier retreated these fish appear to have utilized most, if not all, of the southern glacial outlets in order to spread into the Ontario watersheds. The presence of *Pfrille neogaea* in New Brunswick and in New England suggests that this species probably utilized the St. Lawrence or Champlain channel in its eastward migration as well as the Mohawk-Hudson outlet.

GROUP III

Fig. 18 (p. 38)

Salvelinus fontinalis. Eastern speckled trout.

Range: Eastern Canada from Labrador to the Nelson River; southward in the Alleghanies to northern Georgia and westward from Maine to the Dakotas; in clear, cold streams and lakes.

Catostomus commersonnii. White sucker.

Range: From the Mackenzie River to Hudson Bay and Labrador; southward to South Carolina, Missouri and Colorado; in almost all waters.

Notropis hudsonius. Spot-tail shiner.

Range: Essentially a northern species, ranging from New England and Quebec to Lesser Slave Lake, throughout the Great Lakes basin and in the Hudson Bay drainage at least as far north as 52° 50′ in Ontario, southward on the Atlantic coastal plain to South Carolina (as subspecies *N. h. saludanus*), in the Mississippi Valley to Illinois and Indiana; northward chiefly in large lakes and rivers, but as Dr. Hubbs has pointed out (letter), along the seaboard in warm, lowland, even brackish waters (as subspecies *N. h. amarus*); on the prairies it also occurs in small, shallow lakes and a number in which the salinity ranges from 2500 to 3200 p.p.m.

Rhinichthys cataractae. Long-nose dace.

Range: From Quebec and New Brunswick southward to Virginia; through the Great Lakes and Hudson Bay basin, westward to the, Saskatchewan Valley, the Columbia River basin and British Columbia and south in the Mississippi Valley to the Rio Grande; in swift streams and sometimes along lake shores.

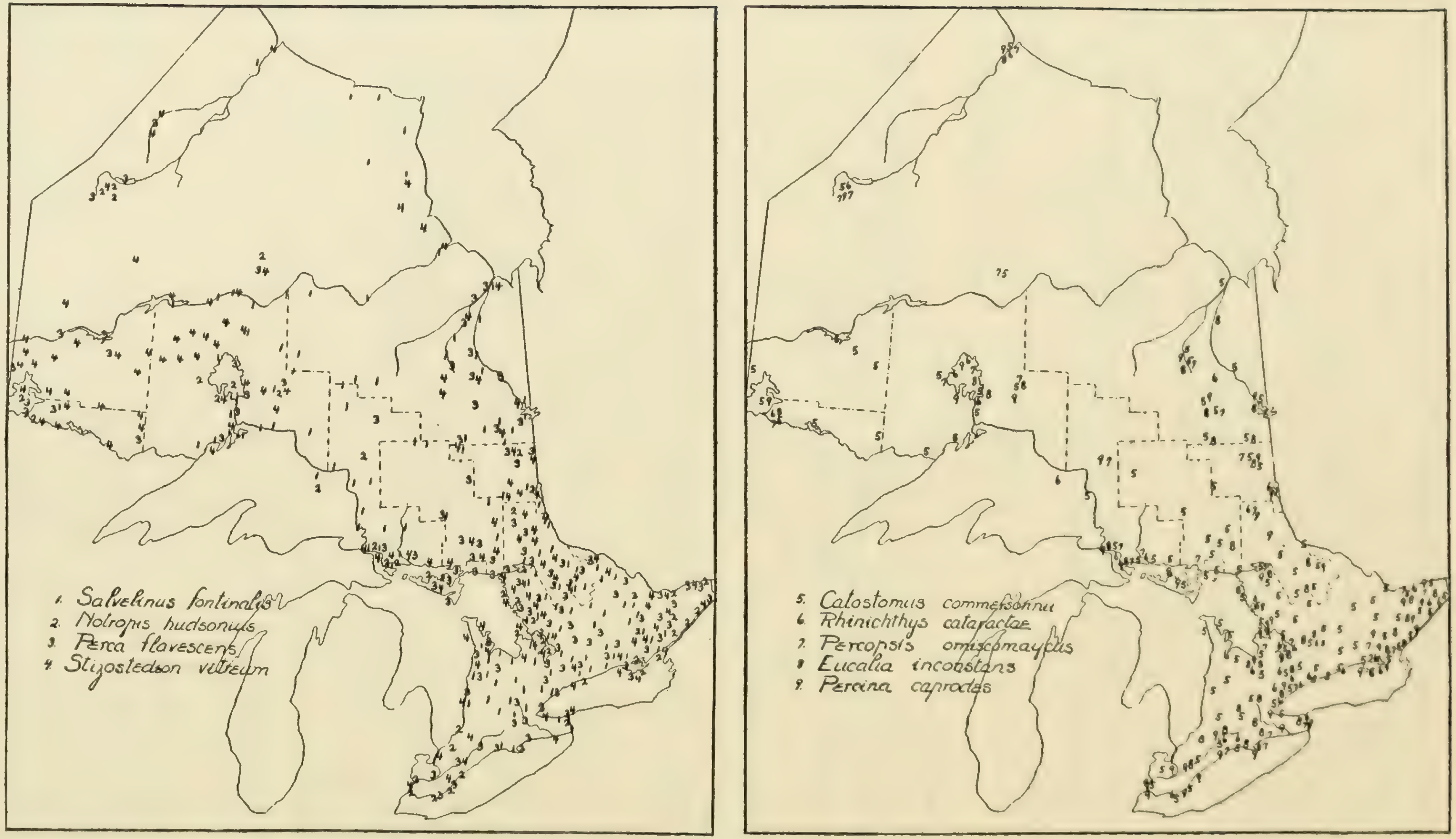


Figure 18. Distributional maps for Group III of the species which are generally distributed in Ontario.

Percopsis omiscomaycus. Trout-perch.

Range: From New England and Quebec west to Kansas and north to the Saskatchewan Valley and Hudson Bay; rare south of the Great Lakes (Dr. Hubbs informs us that he has specimens from the Potomac in Virginia); in larger streams and in lakes.

Eucalia inconstans. Brook stickleback.

Range: In central and southern Canada from the Saskatchewan and Hudson Bay basin to New Brunswick, southward to New York, Illinois and Kansas; chiefly in smaller streams.

Perca flavescens. Yellow perch.

Range: From Nova Scotia to South Carolina in the east, through the Mississippi Valley to Kansas and northern Missouri; northwest to Lesser Slave Lake in Alberta; in lakes and larger streams.

Stizostedion vitreum. Yellow pike-perch.

Range: From New Brunswick to Virginia on the Atlantic coast, through the Great Lakes region and upper Mississippi Valley westward to the Saskatchewan Valley and northward to the Mackenzie River region and Hudson Bay drainage; in lakes and larger rivers.

Stizostedion vitreum glaucum. Blue pike-perch.

The Ontario range of this form is known to include lakes Erie, Ontario, Nipissing, Three-Mile Lake (Muskoka District) and Long Lake (Frontenac County). For a time the blue pike-perch was regarded as a distinct species, *Stizostedion glausum*, but more recently (Hubbs and Lagler, 1941) it has been given subspecific status. These authors suggest that the Lake Ontario "blue pike" may not be identical with the Lake Erie form.

Percina caprodes. Log perch.

Range: From the Hudson Bay slope (known from De Laronde Lake, a tributary of the Churchill River in northern Saskatchewan and from Severn River, Hudson Bay), general in the Great Lakes basin south through the Mississippi Valley to Texas and to Virginia in the east.

(The northern log perch, *P.c. semifasciata*, is the subspecies of Ontario waters (Greene, 1935). It ranges from Minnesota through the Great Lakes to Quebec and Vermont, and intergrades with the southern subspecies, *P.c. caprodes*, all along this line.)

The remaining nine species (fig. 18) which are of general occurrence in Ontario present a variety of problems some of which can best be dealt

with by comparative discussion. The general nature of their Ontario distribution seems to indicate that these fish began their post-glacial dispersal early and followed the retreating glacier rather closely. As the species in question, with the exception of *Catostomus commersonnii* which is of ubiquitous occurrence, show a preference for clear, cool water, it is not likely that they inhabited the waters in close proximity to the foot of the glacier where debris from the melting ice would produce a severe muddy condition. At some distance from the ice front the sediments must have settled out, depending on the nature of the terrain and the water would become sufficiently clear to permit the entrance of such fish as *Salvelinus fontinalis*. As far as the majority of these species is concerned there probably existed an interval of some extent between the time when the northern waters were made available geologically and the time when they became ecologically suitable. The advancing line of fishes would lag some distance behind the retreating ice front but the northward dispersal began early enough to carry these fish beyond all divides which prevented the advance of species which reached them at a later stage.

The ranges of the species in this third group extend to the drainage of the Atlantic coast as well as throughout Ontario and the upper Mississippi Valley. Since their present ranges include both the Atlantic coastal drainage and the Mississippi basin it is possible that the pre-glacial distribution of these fish included both these regions. In this case the retreat of the fishes as the ice advanced would result in the separation of the population into an Atlantic coast element and a Mississippi Valley element, since the Great Lakes region, which formed the connecting link then as now between these two significant regions, lay beneath the glacier. If it is true that these two areas contained populations of the species in question during the glacial period, then the present distribution has been produced by the utilization of all glacial outlets to the south and southeast as the fishes followed the retreat of the ice.

In order to clarify the situation let us assume that there were no members of these species isolated in the Mississippi Valley and that the Atlantic coastal region must be responsible for their present distribution. In such an event, when the ice retreated northward, dispersal probably took place through the Mohawk-Hudson outlet during the different stages in the development of the lake basins. To attain the present distribution all the glacial outlets must have been utilized. Entrance to Lake Erie would have to be attained before the end of the Lake Lundy stage, or by the indirect route through the Algonquin River to Lake Huron and then southward to Lake Erie. Northern Ontario would

receive its population across the divide from Lake Algonquin. The Mississippi representatives of these species would also be derived from the Atlantic centre by dispersal through the outlets from the Great Lakes basins. From the Mississippi Valley the species could extend into Lake Agassiz and the western slope of Hudson Bay. This northwestern extension of the range could also be attained through the Temiskaming outlet of Lake Ojibway and thence across northern Ontario into Manitoba. The occurrence of most of these fish in the Dakotas and the Red River system seems to indicate that the Agassiz outlet to the Mississippi was used in the course of northward dispersal. If these species did come from the Atlantic slope and through the upper Mississippi waters to Lake Agassiz then this most western outlet remained open for a much longer period than has been supposed.

On the other hand, the Mississippi Valley may have been the sole refuge of these species during the ice age. If this has been the case their Ontario distribution would be attained in the same manner as that of the Mississippi forms already discussed. The Atlantic coast members would then be derived from the Mississippi element by dispersal through the Great Lakes basins eastward, through the Mohawk-Hudson, Champlain and St. Lawrence waterways to the Atlantic coastal drainage.

Three species of this group, *Salvelinus fontinalis*, *Notropis hudsonius* and *Stizostedion vitreum*, occur farther south in the Atlantic coastal drainage than in the Mississippi Valley. The Atlantic coast ranges of these fish are similar although *S. fontinalis* occurs mainly in the mountain streams while the other two species extend through the waters of the coastal plain.

The northwestern limits of occurrence of *S. vitreum*, *Perca flavescens* and *N. hudsonius* extend well beyond those of *S. fontinalis*. The pike-perch occurs in the Saskatchewan Valley and northward to the Mackenzie River basin, while the spot-tail shiner has been reported from the Athabaska region and occurs, with the yellow perch, in Lesser Slave Lake, Alberta. The wide range of these fish in both the eastern and northwestern limits of their distribution is probably the result of derivation from a Mississippi as well as from an Atlantic centre of dispersal. Their need for cooler waters than are at present available in the Mississippi region would be satisfied by the presence of the glacier. During glacial times they could no doubt exist much farther south in the Mississippi Valley. Their presence in the Mississippi Valley as well as the wide northwestern distributions of these three types strengthens the view that they have been redistributed from a Mississippi as well as an Atlantic centre.

The eastern speckled trout is noted for its particular choice of habitat in which it shows a definite preference for clear, cool, highland streams.

It is not likely that the lowland streams of the Mississippi Valley would provide suitable refuge for this species during the ice age. The glacial waters, though cool, would be turbid with debris from the moraines. In the Atlantic coastal region, mountain streams of the Appalachian heights south of the ice sheet probably offered favourable habitats for this species at that time just as they do at present. It is suggested by this feature of the ecological requirements of the species as well as by its restricted western dispersal that the eastern speckled trout survived the ice age in the drainage of the Atlantic coast. With the retreat of the glacier dispersal probably took place through the eastern outlets, the Great Lakes and over the divides into the Hudson Bay drainage and the upper Mississippi waters, where suitable habitats are provided in some headwaters.

The remaining three species of this group, *Catostomus commersonnii*, *Rhinichthys cataractae* and *Percina caprodes* are found to occur well southward in both the Mississippi and Atlantic coast areas. The obvious conclusion from so wide a range is that both these regions were centres for post-glacial dispersal of these fishes. This is a simple conclusion as far as the white sucker is concerned but the other two species present more complex problems.

In the case of the log perch the matter is complicated by the fact that this fish occurs in the form of two subspecies, a northern one found north of a line from Minnesota to Vermont, and the typical subspecies south of this line, the two forms intergrading with each other along the border of their ranges. The difficulty lies in explaining the presence of the same subspecies to the north of both the eastern and western centres of dispersal. There is little possibility that the Mississippi and Atlantic populations of *P.c. caprodes* provided two origins for the same northern subspecies. It does not seem improbable that a new subspecies might have arisen during the ice age in the Atlantic drainage where a considerable variety of habitats are offered in the mountain streams and the rivers of the coastal plain. In the more uniform habitat of the lowland type of stream in the Mississippi Valley new types would not be likely to arise. On the basis of this theory the subspecies *semifasciata* probably developed in the northern part of the eastern element of *P. caprodes* during the glacial period. As the ice retreated this new subspecies spread throughout the St. Lawrence and Great Lakes basins, across the divides to the Hudson Bay slope, probably from Lake Algonquin into Lake Ojibway and thence to Lake Agassiz. Southward from the Great Lakes this northern subspecies appears to have entered the upper Mississippi Valley where further southward dispersal has been stopped, perhaps by competition with the southern form. This theory assumes that the Mississippi population of *P.c. caprodes* had not proceeded very far in its northward dispersal before it was stopped by the incoming *P.c. semifasciata.*

The remaining species, *Rhinichthys cataractae*, appears to be more widely established in the regions west of the Mississippi River than any other fish of this group. It is evident that the Mississippi Valley has been one source of redistribution of the long-nose dace. Because of this widespread western occurrence it may be concluded that the presence of this species, even as far south as Virginia, in the Atlantic coastal plain, may have been a result of southward dispersal after penetration into the Great Lakes region from the Mississippi Valley. However, from evidence based on the distribution of typical Mississippi derivatives which were apparently unable to extend their eastern ranges to any extent, such an extensive eastern distribution as shown by *R. cataractae* does not seem possible without an eastern post-glacial source as well. In this event, some of the Ontario representatives of this species may have been derived from the Atlantic coastal population through the southeastern outlets of the post-glacial lakes. A more certain outlook of the problem may be reached when the distribution of subspecies of *R. cataractae* has been studied in detail.

A species of darter, *Boleosoma nigrum*, of which the typical subspecies occurs throughout Ontario, has been omitted from the present discussion because of complicated problems in connection with subspecies, and will be dealt with later as a special case.

From the information given in the preceding pages it may be concluded that species of fishes which are generally distributed throughout Ontario appear to have made use of all the glacial outlets and to have been derived from all three possible centres of post-glacial distribution although the utilization of these areas in order to survive the ice age, and the methods of redistribution have been influenced by the individual requirements of each species.

SPECIES WHOSE DISTRIBUTION IN ONTARIO IS POTENTIALLY GENERAL

Fig. 19 (p. 44)

Moxostoma aureolum. Northern redhorse.

Range: From Lake Champlain and the upper St. Lawrence Valley, through the Great Lakes basin, northward in Ontario at least to the Attawapiskat and Albany drainage of James Bay, and northwest to the Mackenzie River region; in the Mississippi Valley west to Montana, south to Kansas; in lakes and rivers.

Couesius plumbeus. Lake chub.

Range: Through Canada from New Brunswick to the Rocky Mountains, northward in Ontario to Fort Severn on Hudson Bay,

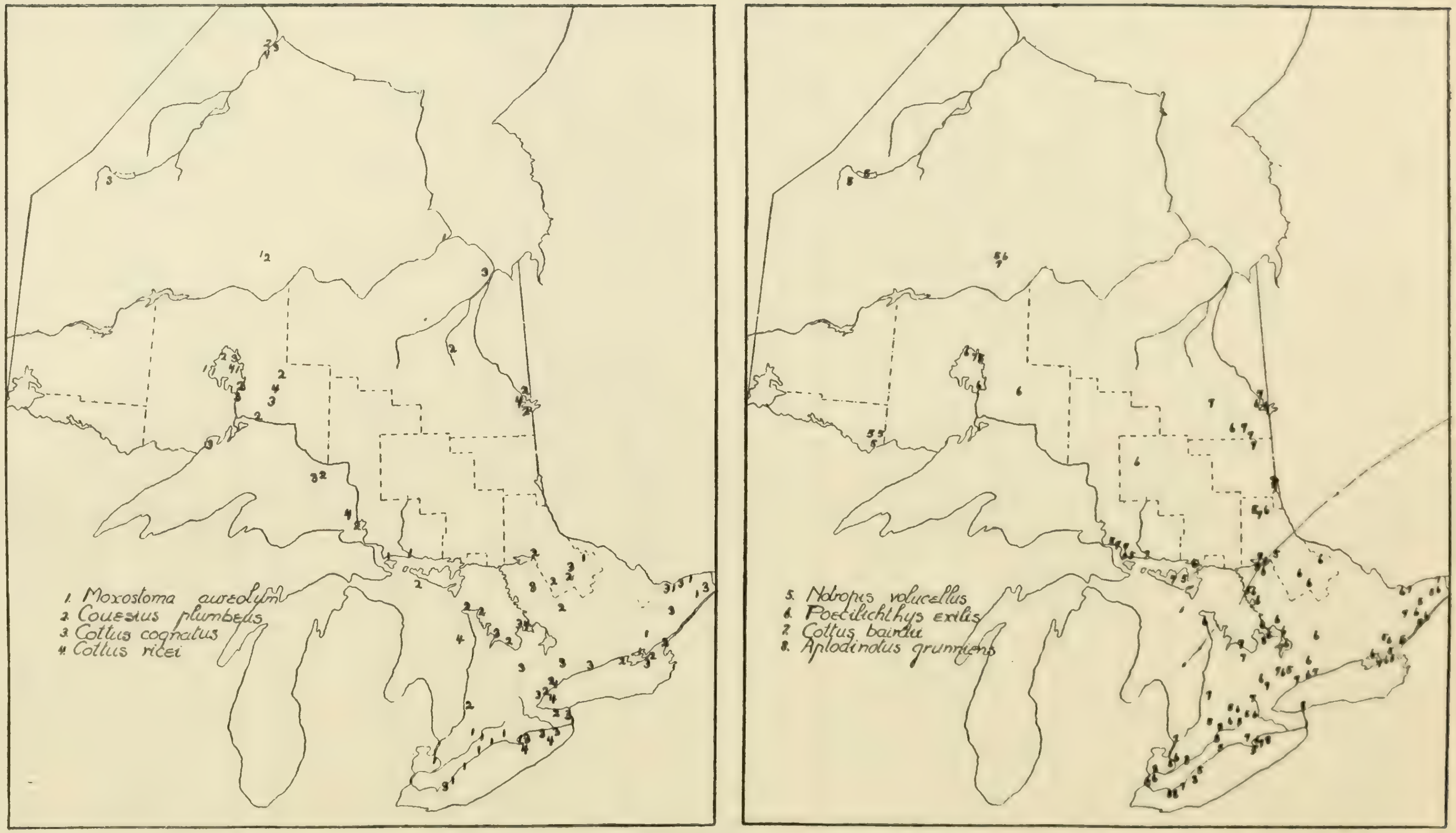


Figure 19. Distributional maps for the species whose distribution in Ontario is potentially general.

northwest to Great Bear Lake, southward to Wyoming, Iowa, New York and Maine. The Ontario population is largely if not entirely subspecies *C. p. plumbeus* which occurs throughout northern Canada chiefly in lakes except when it enters tributary streams in spawning season. The finding of *C. p. dissimilis* in the Keweenaw Peninsula of Michigan (Hubbs and Lagler, 1941) suggests that this form may occur also in Ontario. Its distribution is from the east slope of the Rocky Mountains eastward across the northern part of the Great Plains.

Notropis volucellus. Mimic shiner.

Range: From Lake Champlain to Minnesota, north to at least 52° in the Hudson Bay drainage of Ontario; southward through the Great Lakes and the Mississippi drainage to Alabama and the Rio Grande; in creeks, pools and weedy lakes. The northern subspecies *N. v. volucellus* is the Ontario form. Hubbs and Lagler (1941) include *N. v. buchanani*, a Mississippi Valley form because characters of that form are shown by races in the Lake Erie drainage particularly in Talbot Creek, Ontario.

Poecilichthys exilis. Iowa darter.

Range: Saskatchewan to Quebec and Lake Champlain, north in Ontario to the Attawapiskat drainage of James Bay, southward to Ohio, and southwest to Colorado; in muddy areas of lakes and streams.

Cottus bairdii. Muddler.

Range: From Minnesota eastward to New Brunswick, north in Ontario to the Attawapiskat drainage of James Bay, southward east of the Alleghanies to Virginia, and west of the Alleghanies to Tennessee; in cool creeks and lakes. Two subspecies occur, *C. b. bairdii*, a northern form from Hudson Bay tributaries throughout the Great Lakes region including Lake Erie, at least its western end, but excluding the other Great Lakes, and the inland lakes inhabited by *C. b. kumlieni* (Hubbs and Lagler, 1941).

Cottus cognatus. Slimy muddler.

Range: From Alaska through Canada to Labrador, north in Ontario to Fort Severn on Hudson Bay, southward to Minnesota, the Great Lakes basins and New York, and on the Atlantic slope to West Virginia; in cold streams and lakes.

Cottus ricei. Spoon-head muddler.

Range: From the Saskatchewan River eastward through the Hudson Bay and Great Lakes watersheds, north in Ontario to Fort Severn on Hudson Bay; in cold deeper waters of lakes.

Aplodinotus grunniens. Freshwater sheepshead.

Range: From the Rio Usumacinto in southern Mexico to Lake Winnipeg and Lake Abitibi; in the Rio Grande and other rivers of Texas, throughout the basins of the Mississippi, Great Lakes (except Superior), St. Lawrence and Lake Champlain, absent from Atlantic coastal waters; in large lakes and rivers.

Except in the case of *Aplodinotus grunniens*, the maps for this group (fig. 19 p. 44) exhibit a common characteristic: the occurrence of the species in all the main watersheds of Ontario except the Lake of the Woods. The tendency of most of the species to occur widely in areas west of Ontario as well as their general occurrence in Ontario waters, seems to indicate that geological barriers have not kept these fish out of the Lake of the Woods region. Their apparent absence may be due to our incomplete information or some ecological factor may be responsible.

All three distributional sources appear to have contributed to the occurrence of these fish in Ontario. *Cottus cognatus* is most likely an Alaskan derivative. *Moxostoma aureolum*, *Notropis volucellus*, *Poecilichthys exilis* and *Cottus ricei* seem to have come from the Mississippi Valley. *Couesius plumbeus* and *Cottus bairdii* appear to have been derived from both the Mississippi Valley and the Atlantic coastal plain.

Aplodinotus grunniens has been included in this group because of its wide occurrence outside Ontario. The width of its distribution "through thirty-five degrees of latitude", has been emphasized by Barney (1926), who says it is "perhaps the greatest in point of latitudinal range of any American fresh-water species." Although it is found from tropical rivers, and semi-tropical bayous to northern lakes and streams it appears to be everywhere confined to larger waters. This fact would seem to account for its limited distribution as compared with other species of the group, in Ontario, where, besides the Great Lakes, it is known with certainty only from Lake Nipissing, the Ottawa River and Lake Abitibi. The absence of the sheepshead from Atlantic coastal waters and its wide distribution in the Mississippi Valley suggests its derivation from the latter centre of post-glacial dispersal.

SPECIES WHOSE OCCURRENCE IN ONTARIO IS LIMITED TO THE BASINS OF LAKE ERIE, LAKE ST. CLAIR AND THE SOUTHERN PART OF LAKE HURON

Fig. 20 (p. 47)

Ichthyomyzon fossor. Michigan brook lamprey.

Range: In the Erie, Huron, Michigan, and Superior drainages of Michigan; recorded from the Lake Erie drainage of New York State,

Figure 20. Distributional map of species whose occurrence in Ontario is limited to the basins of Lake Erie, Lake St. Clair, and the southern part of Lake Huron.

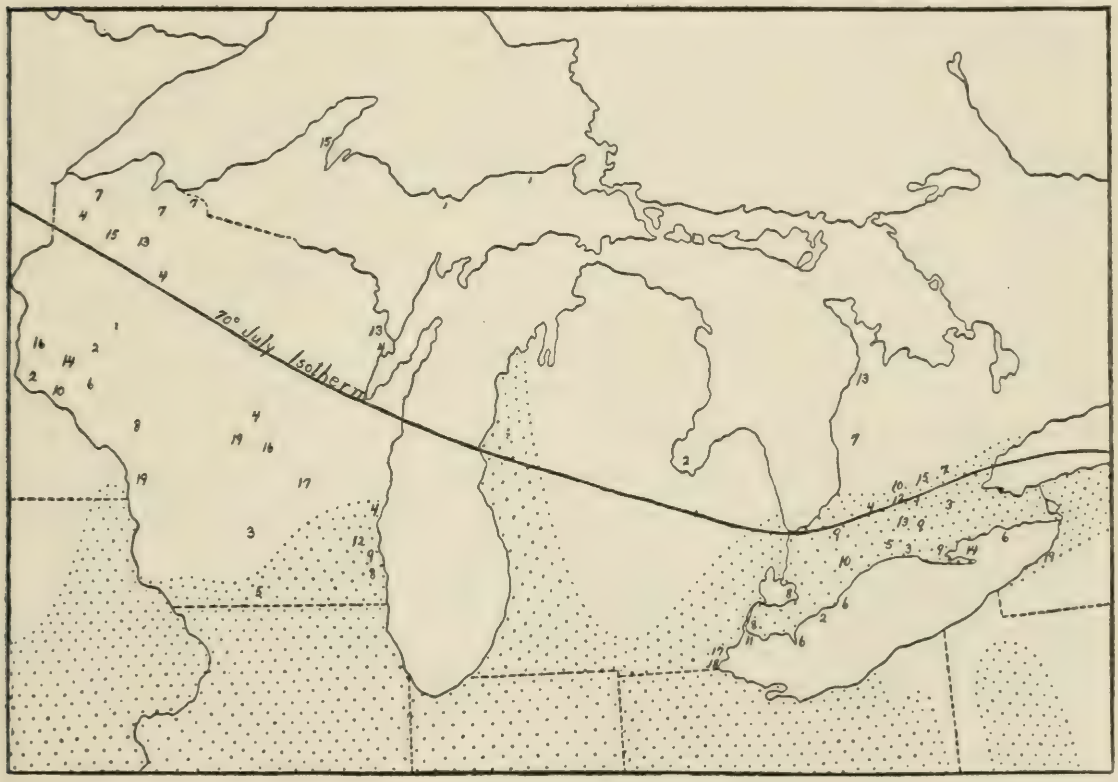


Figure 21. Distributional map showing the northern limits of range of the species of Figure 20, in Ontario, Wisconsin, and in a few cases in Michigan, with their relation to the Carolinian Area (stippled) and the 70° July isotherm.

and from the Mississippi drainage of Wisconsin and Indiana. This lamprey has never been taken in lakes and spends its whole life in creeks and small rivers.

For Ontario there is only one record of the occurrence of this species, a specimen in the collection of the Royal Ontario Museum of Zoology, taken from a small tributary of the Thames River near Harrington.

From the present distribution it seems likely that the Fort Wayne, Chicago and St. Croix outlets have been utilized in dispersal. However, the Fort Wayne outlet of the Lake Erie basin appears to have been the only channel through which this fish entered Ontario waters from the Mississippi drainage where it must have lived during the glacial period.

Lepisosteus productus. Spotted gar.

Range: Southward from the Great Lakes, generally common throughout the Mississippi Valley.

In Ontario, this species occurs only in the Lake Erie drainage. One specimen, now in the Royal Ontario Museum of Zoology collection, was taken near Merlin, Kent County. With respect to its Ontario distribution the Fort Wayne route was probably the channel by which this form extended its range northward from the Mississippi Valley.

Moxostoma duquesnii. Black redhorse.

Range: Southern Wisconsin to southern Ontario and Pennsylvania, southward through the drainage of the Gulf of Mexico to northern Georgia, southern Arkansas and eastern Oklahoma; medium-sized, clear rivers.

There are only three records of this species from Ontario waters: Catfish Creek near Aylmer, Elgin County (Royal Ontario Museum of Zoology collection), Catfish Creek at Jaffa, Elgin County, and Cedar Creek, a tributary of the Grand River, between Princeton and Paris, Brant County (Hubbs and Brown, 1929).

Collections in the basin of Lake Michigan have shown that this species has used the Chicago outlet in its post-glacial redistribution. With respect to Ontario, as shown by the occurrence of the species in the Lake Erie drainage, it appears that only the Fort Wayne outlet has been effective in carrying the species into Ontario waters from the Mississippi Valley.

Moxostoma erythrurum. Golden redhorse.

Range: Lake Huron and Lake Erie drainages of southern Ontario, through Michigan and Wisconsin southward in smaller streams and rivers of the Mississippi Valley to Oklahoma, Arkansas and Georgia.

There is little difficulty in explaining the distribution of this species

in the Ontario drainages of Lake Erie, Lake St. Clair and the southern part of Lake Huron. Utilization of the Fort Wayne outlet probably accounts for the Lake Erie occurrence, while records for Lake St. Clair and southern tributaries of Lake Huron may be attributed to either the Fort Wayne outlet or the Chicago outlet. Use of the Chicago outlet is believed definitely established by Michigan records. However, utilization of the Chicago-Ubly channel would have required the fish to follow the retreating glacier quite closely. In view of the restricted distribution in Ontario, it seems likely that this species entered Ontario waters at a stage when the cold glacial waters had moved farther northeastward and only the Fort Wayne outlet was available. There is also some evidence that the St. Croix outlet has carried this species into the drainage of Lake Superior (Greene, 1935).

Erimystax dissimilis. Spotted chub.

Range: From the Wisconsin and Lake Erie drainage of Ontario southward to the headwaters of the Tennessee and westward to Oklahoma and Kansas; a river-channel fish.

This species is known in Ontario only from the Thames River, Elgin County. It seems to have crossed the divide from the Mississippi Valley by only the Fort Wayne outlet.

Hubbs and Brown (1929) in reporting this species from the Thames River at Muncey Indian Reserve say "This locality; the northernmost for the species . . . remains the only record for Canada. It is one of the southern types which appears to have made use of the Detroit River distribution-portal."

Hybopsis storerianus. Silver chub.

Range: Through the larger streams of the Lake Erie basin southward to Tennessee and west to Arkansas, Nebraska, eastern Wyoming, and north to southern Manitoba; a silt-water fish.

There are four records of this fish from Ontario waters. Dymond (1922) lists it from Point Pelee, Lake Erie. Specimens in the Royal Ontario Museum of Zoology collection record its occurrence along the north shore of Lake Erie at Merlin, Rondeau and Nanticoke. The only route used by this species to enter Ontario waters seems to have been the Fort Wayne outlet. Greene (1935) and Eigenmann (1895) record this fish from the Red River basin of Canada. Although a southern species, it must have been able to withstand the northern conditions sufficiently to pass beyond the divide while Lake Agassiz was still in existence.

Nocomis biguttatus. Horny-head chub.

Range: From eastern North Dakota, Wisconsin, the lower Great Lakes and the Hudson drainage of New York southward in tributaries of the Mississippi to the Ohio Valley and Oklahoma; in clear streams with gravel riffles.

The restricted occurrence of this species in Ontario is indicated on the accompanying map. The Fort Wayne outlet appears to have been utilized in entering southern Ontario, while use of the Chicago-Ubly channel seems doubtful, as in the case of *Moxostoma erythrurum*.

Opsopoeodus emiliae. Pug-nose minnow.

Range: In sandy, lowland streams, lakes and ponds, from the Lake Erie drainage and southern Indiana through the Mississippi Valley to Texas and southeast to Florida; in sluggish, usually weedy waters.

While this species is fairly common in Michigan tributaries of Lake Erie, only two records have been obtained for Ontario waters. Doan (1936) collected two specimens in a small artificial drainage opening into Mitchell's Bay, Lake St. Clair, and Dr. Hubbs took it in the Detroit River off Fighting Island in 1940. The occurrence of this species in the Lake Michigan drainage of Indiana and in the Lake Erie-Lake St. Clair region, but not between, indicates the use of both the Chicago and other Erie-basin outlets.

Schilbeodes miurus. Brindled madtom.

Range: From tributaries of Lake Michigan through the Mississippi Valley to Louisiana and the Lower Missouri; occurring usually in running streams and creeks with a clean bottom and a swift current.

The distribution of this species in Ontario waters is represented by four records. Specimens in the Royal Ontario Museum of Zoology collection were taken in Catfish Creek near Aylmer, and in the Sydenham River near Alvinston. Hubbs and Brown (1929) record it from the Sydenham River east of Sarnia and from Dedrick's Creek near Port Rowan.

Forbes and Richardson (1920) attributed the apparent absence of *S. miurus* north of the Kaskaskia system in Illinois to ecological factors and competition with *Noturus flavus*. The Ontario records extend the northern limits of the species. Here also it might be suggested that further northward distribution is prevented by ecological factors. In any case the species appears to have utilized the Fort Wayne outlet in order to attain its present Ontario distribution.

Etheostoma blennioides. Green-side darter.

Range: From lakes Ontario and Erie to Pennsylvania, North Carolina and the lower Alabama basin, west to South Dakota, Kansas and Missouri and the Red River in Arkansas; inhabiting swift, clear brooks, most often in rocky riffles where there is a vigorous growth of algae.

In Ontario this species has been collected only in waters tributary to Lake St. Clair and Lake Erie. The Fort Wayne outlet was probably used to produce this distribution. There are records of the occurrence of the green-side darter in the New York tributaries of Lake Ontario as far east as the Oswego River (Greeley, 1926, 1927). It is possible that this species spread eastward from the Mississippi-Maumee passage into the New York tributaries of Lake Ontario at the time when the eastern arm of Lake Warren extended along the ice lobe into the southern part of the Ontario basin. It is not likely, however, that a species such as *E. blennioides*, which appears limited to a warm zone in Ontario, would follow the retreat of the ice so closely. Distribution into the New York drainage from the Mississippi Valley was possible at a later stage when Lake Lundy included the Lake Erie basin and part of that of Lake Ontario. There seems to be no reason why dispersal into the Ontario tributaries of Lake Ontario has not taken place. The occurrence of this species in Ontario needs further investigation before anything further can be said. As the distribution stands at present it appears that this darter entered the Lake Erie and Lake St. Clair drainage via the Fort Wayne outlet and has extended its range no further in Ontario.

Cottogaster copelandi. Channel darter.

Range: From Lake Champlain and the New York tributaries of the upper St. Lawrence River through the Great Lakes region to Lake Huron, south in the Gulf drainage to the Black Warrior River, and westward to Missouri; in clear brooks.

This species has only recently been added to the fauna of Ontario. Dr. C. L. Hubbs, collecting in the Detroit River area in 1940, took some channel darters about one mile south of Amherstburg, Essex County. This species seems to have made use of only the Fort Wayne outlet in its northward dispersal into Ontario waters. The apparent absence of *C. copelandi* from the Ontario waters east of Lake Erie is even more striking than in the case of *E. blennioides*, since the former occurs in New York tributaries of the St. Lawrence River but has not been found in nearby Ontario tributaries. The distribution of the channel darter, however, shows that the theory of a Mississippi Valley derivation of the New York occurrences of *E. blennioides* is quite logical.

Ammocrypta pellucida. Northern sand darter.

Range: From Quebec in the vicinity of Montreal, northern Vermont and New York to southern Ontario and southeastern Michigan; southward in clear sandy streams and on the sandy shoals of a few lakes to West Virginia and Kentucky.

Whether this species presents the same problem as *Etheostoma blennioides* in its distribution is not known. In Ontario the sand darter occurs in tributaries of Lake Erie, Lake St. Clair and the southern part of Lake Huron, and presents another example of dispersal through the Fort Wayne outlet from the Mississippi Valley, with doubtful use of the Chicago channels. This fish is generally the only inhabitant of sand bars and the sandy reaches of larger streams. Such a restricted habitat may be partly responsible for its limited distribution, but in view of the fact that sandy streams are common beyond the northern limits of the species in Ontario, some other factor must be effective in preventing further northward dispersal.

Hadropterus maculatus. Black-side darter.

Range: Southern parts of Ontario and Manitoba, extending in the Mississippi Valley to Oklahoma and Tennessee; in streams with gravel beds and riffles which are required at spawning time.

The distribution of this species in Ontario waters is restricted to the Erie, St. Clair and south Huron tributaries in southwestern Ontario. Most of the records so far obtained are from the area to which several species such as *E. blennioides* are restricted. One record, however, has been obtained from the Saugeen River, a tributary of Lake Huron at the foot of Bruce Peninsula, which is some distance north of the other occurrences. Here again the Fort Wayne channel may alone be responsible for this distribution. Utilization of the Chicago Channel is doubtful as in the case of *Moxostoma erythrurum*. Although not yet recorded from western Ontario in the Lake of the Woods region, this species is known to occur in the Red River system of North Dakota draining into Lake Winnipeg (Hankinson, 1929) and in southern Manitoba at Winnipeg (Eigenmann, 1895). The Lake Agassiz outlet must have been used by this species, but there is no indication that the St. Croix outlet assisted the distribution in any way.

Lepomis cyanellus. Green sunfish.

Range: Southern Ontario and western New York to South Dakota and southward west of the Alleghanies through the Mississippi Valley to Georgia and Mexico.

This species is a typical Mississippi Valley form occurring in small

sluggish brooks. It is abundant in the southern part of its range, but less common northward.

There are two records of this species for Ontario; Jones Lakes near Stratford (Royal Ontario Museum of Zoology collection), and Little Lakes, headwaters of the Avon River near Stratford, Perth County (Hubbs and Brown, 1929). With respect to the Ontario distribution apparently only the Fort Wayne outlet has been utilized. This has also resulted in the fairly common occurrence of *L. cyanellus* in the U.S. drainage of Lake Erie. Greene (1935) gives evidence for believing the Chicago outlet was traversed by this species while isolated records at a more northern latitude very near the Lake Superior watershed, and in the Lake Superior drainage of Michigan, seem to indicate probable use of the St. Croix outlet and "support the theory that an earlier post-glacial period was warmer than the present."

The following four species are included here provisionally. Although recorded from United States tributaries of Lake Erie they have not yet been taken in Ontario waters.

Erimyzon oblongus claviformis. Western chubsucker.

Range: West of the Alleghany Mountains, from the lower Great Lakes above Niagara Falls, (southwestern Michigan and northeastern Ohio) to Oklahoma and Alabama; chiefly in creeks.

The eastern subspecies (*E. o. oblongus*) found in the Atlantic coast drainage from the Maritime Provinces to Virginia, in the Great Lakes is confined to the eastern part of the Lake Ontario basin. The western subspecies has been taken in the Lake Erie drainage of Ohio and Michigan (Dr. C. L. Hubbs, letter, Royal Ontario Museum of Zoology, Feb. 26, 1941) and probably utilized both the Chicago and Fort Wayne outlets in its northward dispersal.

Minytrema melanops. Spotted sucker.

Range: From the basins of Lake Erie and Lake Michigan to Florida and westward to Kansas and Texas; in sluggish rivers.

Dr. Hubbs (letter, Royal Ontario Museum of Zoology, Feb. 26, 1941) states that the spotted sucker has been taken in Lake Erie and its tributaries in Michigan; later taken in Lake St. Clair. The Fort Wayne and Chicago outlets have not likely been utilized in producing this northerly distribution.

Placopharynx carinatus. River redhorse.

Range: St. Lawrence River in the vicinity of Montreal (Vladykov,

1942) and from Michigan to Tennessee, Georgia and Arkansas; in the larger streams.

This species has been taken in the Detroit River, Michigan, (Dr. C. L. Hubbs, letter, Royal Ontario Museum of Zoology, Feb. 26, 1941) and may have utilized the Fort Wayne outlet, although such restricted occurrence north of the outlet could be taken to indicate that the species reached the divide separating the Mississippi waters from the Great Lakes after the postglacial outlets had become extinct. In this event the present occurrence of the river redhorse in the Detroit River may be attributed to the Ohio-Erie canal opened in recent times. Had the Fort Wayne outlet been the means of dispersal we would expect the occurrence of this fish in the Lake Erie basin to be more extensive than it appears at present. Future collections may lead to a more decisive explanation.

Aphredoderus sayanus gibbosus. Pirate-perch.

Range: From South Dakota, southern parts of Minnesota, Wisconsin and Michigan, southern tributaries of Lake Ontario, southward to Texas.

The pirate-perch has been collected from a stream draining into Lake Erie in New York State (Greeley, 1928), and also occurs in southern Wisconsin (Greene, 1935). The Lake Erie occurrence appears to have been the result of dispersal through the Fort Wayne outlet.

The apparent absence of these four species from Ontario waters may be due to ecological barriers, or, on the other hand, these fish may have passed through the Fort Wayne outlet at a late period in its existence, as Hubbs and Brown (1929) suggested, and have not had time to distribute themselves widely through the Lake Erie basin. This time factor is the least tenable of the solutions since there would seem to have been plenty of time since the closing of the Fort Wayne outlet for these fish to have spread into the geologically available waters of the lower Great Lakes.

From the discussion of their individual distribution it is seen that all of the fifteen species which, in Ontario, occur only in the southwestern tip of the province (fig. 20, p. 47) as well as the four provisional species, are typical representatives of the fauna of the Mississippi Valley. These species appear to have utilized only the Fort Wayne outlet in entering the basins of lakes Erie and Ontario. In the case of *Moxostoma erythrurum*, *Nocomis biguttatus*, *Ammocrypta pellucida* and *Hadropterus maculatus*, whose ranges extend into tributaries of Lake Huron, dispersal may have begun somewhat earlier than with the species of more limited distribution although utilization of the Chicago outlets seems doubtful, as has been stated earlier.

The Atlantic coastal drainage contains representatives of one of the species in this group: *Aphredoderus sayanus* (New York to Florida). This type appears to have had an Atlantic coast centre of post-glacial

redistribution as well as a centre in the Mississippi Valley. However, the northward dispersal through the Atlantic coastal plain has been limited. No derivatives of the eastern populations of this species are found in Ontario, and, no contact has been established through the southeastern post-glacial outlets with derivatives of the Mississippi populations of the same species. On the other hand, three of the species which had only a Mississippi centre of dispersal have succeeded in penetrating some distance eastward in the United States drainage of Lake Ontario and the St. Lawrence River. *Nocomis biguttatus* occurs in the Oswego drainage of New York (Greeley, 1928), *Ammocrypts pellucida* is reported from the waters of northern New York State and according to Dr. Hubbs, as far east as the Champlain drainage of Vermont, while *Cottogaster copelandi* has been taken in Lake Champlain (Greeley, 1929).

A collective examination of the distribution of the fishes of this group in Ontario waters, leads to the conclusion that, except for the single record of *H. maculatus* from a tributary of Lake Huron at the foot of Bruce Peninsula, all the distributional points lie within a definite region in southwestern Ontario. We are thus confronted with the problem of why so many species are thus restricted when the distribution of *H. maculatus* shows that dispersal to more northern tributaries of Lake Huron has not been made impossible by any geological factor. It may be argued that the black-side darter began its dispersal earlier than the other species and hence has been able to proceed farther north in the time which has elapsed since the final withdrawal of the ice. Nevertheless, the 25,000 years since the close of the ice age would seem to provide ample time for the other species to extend their ranges into all available habitats at least in the Lake Huron basin.

Thus, the distribution of the species of this group presents two main problems: first, the restricted northern dispersal of some types in the Atlantic coastal region and the consequent absence of derivatives from this centre in Ontario waters; and second, with which we are chiefly concerned, the restricted occurrence in Ontario of Mississippi derivatives, some of which have been able to extend their ranges eastward into the United States drainage of Lake Ontario and the St. Lawrence River.

As far as the Province of Ontario is concerned the species under consideration are found only within the Carolinian Faunal Area of the Upper Austral Zone of Merriam. This area extends from the United States into the southern tip of Ontario and is characterized by a warmer climate together with a flora and fauna quite distinct in many respects from that of the territory to the north. An examination of the more general distribution of the fishes concerned reveals that the northern limit of occurrence of these species in Wisconsin (Greene, 1935) is in most cases, a considerable distance to the north of the range in Ontario,

and well beyond the limits of the Carolinian Area as outlined for that state (figs. 21 and 23). In Minnesota and North Dakota the northern limits of the species are still farther north and still farther away from the Carolinian Area, extending in a few instances into the Canadian Zone. *H. maculatus* and *Hybopsis storerianus*, although not recorded from Ontario waters near the western boundary of the province, occur as far north as Winnipeg (Eigenmann, 1895) in the Red River system beyond the divide separating the Mississippi watershed from that of the northern slope. Here, as in southern Ontario, *H. maculatus* exhibits its tendency to range beyond the northern limits of the other species of the group. It is also significant that *H. storerianus* whose Ontario distribution is definitely restricted, had, in the west, succeeded in extending its range beyond the divide while the Agassiz outlet was still in existence. With regard to the eastern populations, New York, in the Carolinian Area, marks the most northerly limit of the range of *Aphredoderus sayanus*. On the other hand, although the reports of *A. pellucida* from northern New York State come from the region just south of Lake Ontario and lie within the Carolinian Area, farther east the range of this species extends into Quebec near Montreal and Vermont, in the Alleghanian Area. Also *C. copelandi* has been recorded from Lake Champlain in the Alleghanian Area. It is obvious that the extent of the Carolinian Area as it is outlined by Merriam has no relation to the facts of fish distribution in Wisconsin and farther west or in the Lake Champlain region, although it might appear to do so for Ontario and parts of New York State.

The fact that the limits of the ranges of several species reach a more northern latitude as they are traced westward might be considered a simple time relation to the withdrawal of the glacier which is believed to have retreated in a general northeasterly direction. The western waters would be open to dispersal and have a sufficiently high temperature to permit entrance of fishes from the south at an earlier date than the eastern waters. In other words, the advancing line made by fishes extending their ranges northward, would, if the relative time factor were the active principle, have been parallel to the retreating ice front. Are we to assume, then, that the existing limits of range, extending in a line towards the northwest is merely the present status of a still continuing dispersal? Such an assumption would require us to ignore the more northerly occurrence of *A. pellucida* and *C. copelandi* in the eastern parts of their range. It is evident that a more satisfactory explanation for the limitation of northward dispersal must be sought.

In Wisconsin and North Dakota, most of the species of this group occur in the waters of Mississippi slope of the watershed and few have succeeded in crossing the divide into the Lake Winnipeg and Lake Superior basins. The fact that such species as *H. storerianus* have

succeeded in crossing this divide and the presence of this and other species in the Lake Erie and Lake Michigan drainages indicates that the northward dispersal occurred while the outlets were still open. As previously stated, if ecological factors are not active, the species which have limited distribution in Ontario have had sufficient time to reach a latitude in this province at least comparable to, if not beyond their northern limits in Wisconsin and Minnesota where the divide between the Mississippi and Great Lakes watersheds appears to be the barrier to further distribution. There is no apparent reason in relation to time or geological barriers for the limited occurrence of so many species in the drainage of southern Ontario.

Having thus removed the explanation of the restricted distribution of these fishes in Ontario from connection with time or geological barriers, we turn to ecology for a solution of the problem.

A comparison of isothermal maps with the line of northern limit of range of the species of fish concerned has shown that while the isotherms given for fall, winter and spring, as well as for the whole year, appear to have no relation to the matter at hand, the line of northern limit of range for these species seems to follow fairly closely the 70° isotherm for July (fig. 21, p. 47). This isotherm crosses Ontario through the northern distributional points of the fishes of this group and extends in a more northwesterly direction through Michigan, Wisconsin and Minnesota. The northern range limits of the species in Wisconsin (Greene, 1935) agrees reasonably well with the northwesterly course of the isotherm as seen in the accompanying map, and it is interesting to note that the species which are found north of the isotherm in both Ontario and Wisconsin are identical with only two exceptions. Continuing toward the northwest the isotherm passes close to the northern limit (Winnipeg) of *H. maculatus* and *H. storerianus* in Manitoba and that of most of the other species in North Dakota. East of Ontario the isotherm, after crossing Lake Ontario and curving northward through New York State to Lake Champlain, reaches the Atlantic Coast in the region of Long Island. It is suggestive that the range of the Atlantic coast population of *A. sayanus* reaches its northern limit at approximately this point. Still more significance may be given to the northeasterly trend of the ranges of *A. pellucida* and *C. copelandi* as they are traced eastward from Ontario.

Although there are exceptions which do not agree with this theory, as in the case of *Ichthyomyzon fossor* (Hubbs and Trautman, 1937) and *Lepomis cyanellus* (Greene, 1935) whose northern limits in Michigan extend to the Lake Superior watershed, in general the northward dispersal of the group seems to be limited by the highest summer tempera-

tures of the regions in which they occur. On this basis, the restricted distribution of certain species in Ontario may be attributed to the requirement by these species of a certain summer maximum of temperature which will provide them with the necessary conditions for reproduction and growth.

SPECIES WHOSE OCCURRENCE IN ONTARIO EXTENDS BEYOND THAT OF THE PRECEDING GROUP TO INCLUDE THE BASINS OF LAKE ONTARIO, THE UPPER ST. LAWRENCE RIVER AND GEORGIAN BAY

Fig. 22 (p. 59)

Entosphenus lamottenii. American brook lamprey.

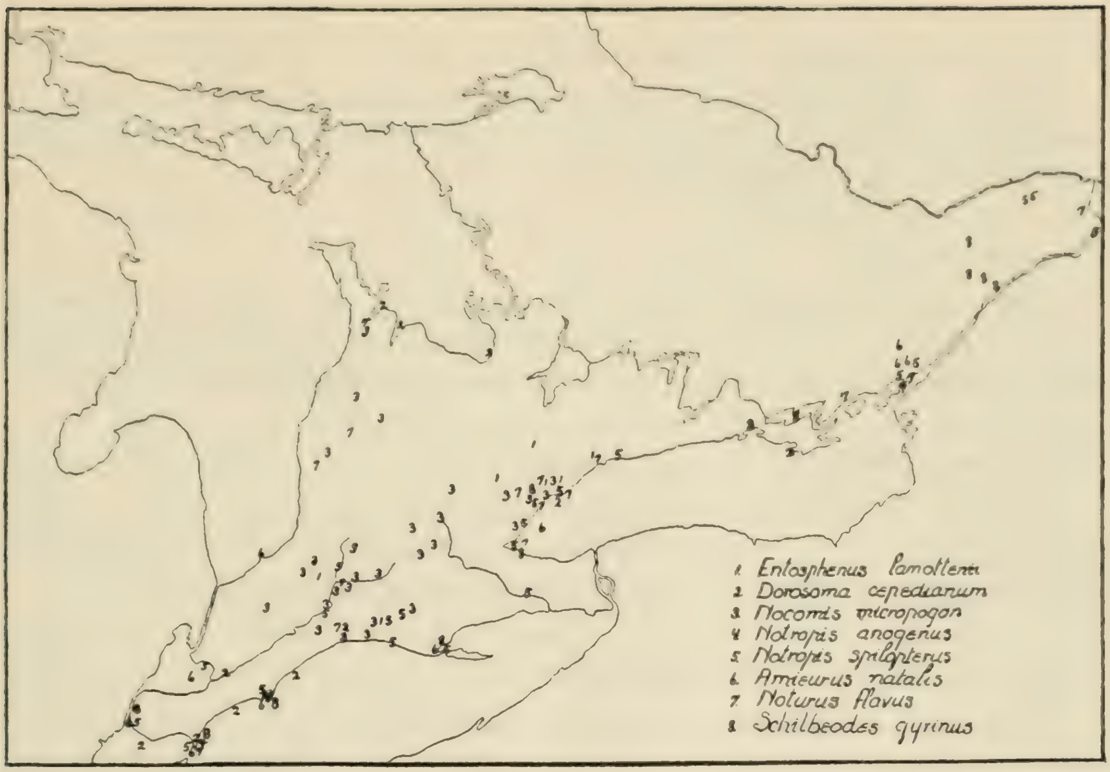
Range: From western New York and southern Ontario to Minnesota southward in the Mississippi Valley to Tennessee and Missouri; on the Atlantic slope from Connecticut to Maryland; in creeks.

Dorosoma cepedianum. Gizzard shad.

Range: From Nebraska and Minnesota eastward through lakes Huron, Erie and Ontario basin to the Ohio valley in Pennsylvania, southward in the Gulf drainage to northern Mexico, and along the Atlantic coast from Florida to New Brunswick; in estuaries, lakes and large rivers.

The wide occurrence of the gizzard shad in both the Mississippi Valley and the Atlantic coastal plain suggests that, as in the case of other species of similar and even more limited distribution, the Chicago-Ubly, Maumee and Mohawk-Hudson outlets have been the means of access to Ontario waters. Statements of other writers have cast some doubt on the utilization of glacial outlets by this species. Hubbs and Lagler (1941) suggest that Milner's reference to the occurrence of the sawbelly, *Pomolobus chrysochloris*, in Lake Erie, may be based on reports by fishermen and may in reality refer to the gizzard shad which is still generally known by the name "saw-belly" in Lake Erie. Jordan and Evermann (1896) observe that this species was "introduced into Lake Michigan and Lake Erie."

The general view appears to be that the occurrence of *D. cepedianum* in the Great Lakes is not a natural one. This fish may have been slow in its post-glacial redispersal and reached the divide too late to make use of the Fort Wayne outlet. In this event, the Ohio-Erie Canal, opened in 1832, and the Erie Canal, opened in 1845, may have provided access to the Great Lakes.



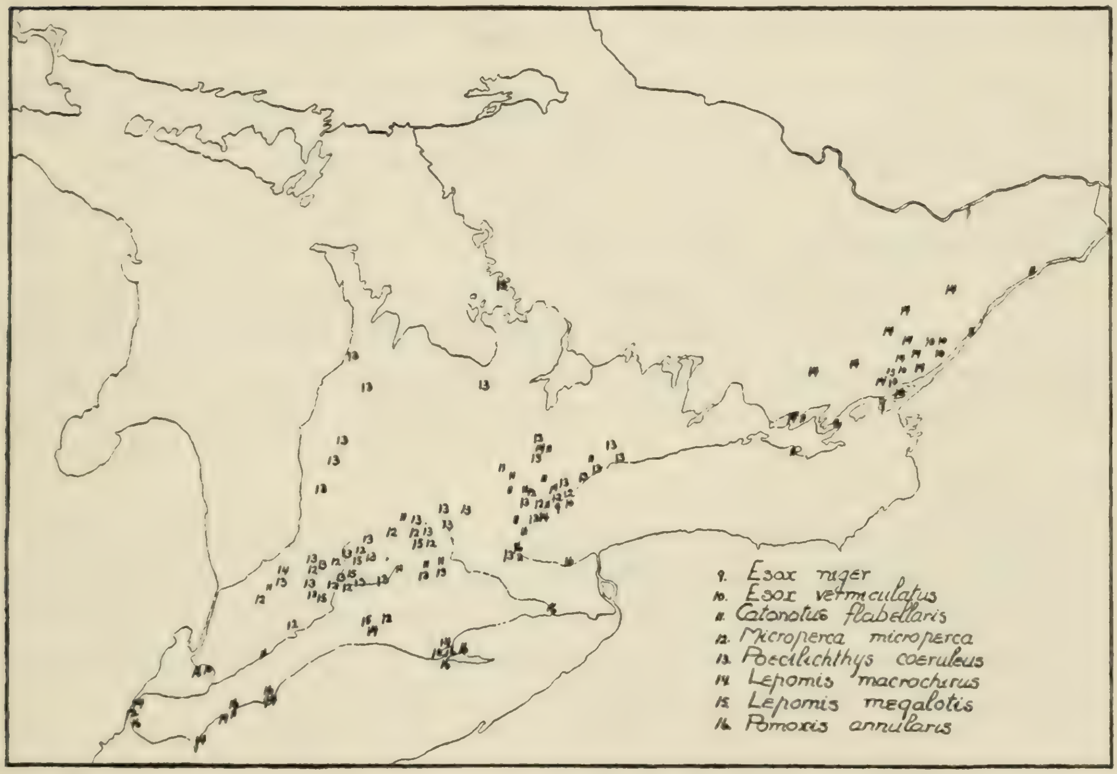


Figure 22. Distributional maps of species whose occurrence in Ontario extends beyond that of the preceding group to include the basins of Lake Ontario, the upper St. Lawrence River and Georgian Bay.

Nocomis micropogon. River chub.

Range: From southern Michigan and southern Ontario southward west of the Appalachian Mountains to Virginia, Georgia and Alabama; in clear streams and rivers.

Notropis anogenus. Pug-nose shiner.

Range: From eastern North Dakota, Minnesota and Iowa eastward through the lower Great Lakes basins to the St. Lawrence drainage of New York and southeastern Ontario; in clear, weedy lakes.

Notropis spilopterus. Spot-fin shiner.

Range: From Lake Champlain through the lower Great Lakes drainage to eastern North Dakota, southward on both sides of the Appalachians to Maryland and Alabama; in lakes and rivers.

Ameiurus natalis. Yellow bullhead.

Range: North Dakota through the Great Lakes region to New Jersey, south on the Atlantic slope to Florida and in the Mississippi Valley to Texas; in clean streams and lakes.

Noturus flavus. Stonecat.

Range: From Lake Champlain and the upper St. Lawrence drainage through southern Ontario, west to Manitoba, southward in the Gulf drainage to Alabama and Oklahoma; chiefly in riffles of streams.

Schilbeodes gyrinus. Tadpole madtom.

Range: From New Hampshire westward through the upper St. Lawrence valley and southern Ontario to North Dakota, southward on both sides of the Appalachians to Florida and Texas; in weedy, mud-bottomed streams.

Esox niger. Chain pickerel.

Range: From New Brunswick to the St. Lawrence and Lake Ontario drainages, southward in the Atlantic coastal plain to Florida; in the Mississippi Valley confined to the southern lowlands along the Gulf and northward to southeastern Missouri and the lower parts of the Tennessee River system; in quiet weedy waters.

Esox vermiculatus. Mud pickerel.

Range: Southern Wisconsin to southern Ontario, the St. Lawrence River and Lake Champlain, southward in the Mississippi Valley to Texas; in lowland streams.

Catonotus flabellaris. Fantail darter.

Range: From the Mohawk River, Lake Champlain and the Upper St. Lawrence valley westward through southern Ontario to Minnesota and Iowa, and southward in the eastern Ohio valley to North Carolina and Alabama; on gravelly-bottomed small streams and lakeshores. The Ontario form is *C. f. flabellaris*.

Microperca microperca. Least darter.

Range: From Minnesota to southwestern Ontario, south to Kentucky, Arkansas and Oklahoma; in quiet, weedy waters of streams and lakes. The Ontario form is *M. m. microperca*.

Poecilichthys caeruleus. Rainbow darter.

Range: From Minnesota to southwestern Ontario and New York, southward to Alabama and Arkansas; in gravelly riffles of streams. The subspecies found in Ontario is *P. c. caeruleus*.

Lepomis macrochirus. Bluegill.

Range: From Minnesota, southern Ontario and Lake Champlain southward in the Mississippi Valley to Georgia and Arkansas; in weedy lakes, ponds, and streams. The Ontario form is *L. m. macrochirus*.

Lepomis megalotis. Long-ear sunfish.

Range: From Minnesota through southern Ontario to western New York, southward in the Gulf drainage to Mexico and Florida; in clear lakes, ponds and streams. The Ontario form is *L. m. peltastes*.

Pomoxis annularis. White crappie.

Range: From Minnesota and southwestern Ontario southward to Texas and Alabama, northward on the Atlantic slope to North Carolina; in turbid streams and lakes.

Most of the species of this group (fig. 22, p. 59) (*Notropis anogenus*, *Noturus flavus*, *Esox vermiculatus*, *Microperca microperca*, *Catonotus flabellaris*, *Poecilichthys coeruleus*, *Lepomis macrochirus*, *Lepomis megalotis*, *Pomoxis annularis*) appear to have entered Ontario waters from only the Mississippi Valley centre, probably utilizing both the Chicago-Ubly and Fort Wayne connections, and to some extent have succeeded in dispersing beyond the limits of range of those Mississippi derivatives considered in the preceding group. *Dorosoma cepedianum* has already been discussed as a probable canal derivative.

Two species, *Entosphenus lamottenii* and *Notropis spilopterus* are well

represented in the Mississippi basin and occur as far south as Maryland on the Atlantic slope. The Chicago and Fort Wayne channels have probably been used by the Mississippi migrants. Dr. Hubbs has expressed the opinion that these species had an Atlantic coastal origin as well as a Mississippi one.

Three species (*Nocomis micropogon*, *Ameiurus natalis* and *Schilbeodes gyrinus*) occur well southward in the Mississippi Valley and the Atlantic coastal plain. Both centres of distribution appear to have contributed to the Ontario populations of these species. *Esox niger* probably came only from the Atlantic side.

Thus, although the Atlantic slope centre has contributed to the Ontario populations of some of the species of this group, others seem to have come from the Mississippi Valley through the Fort Wayne and perhaps the Chicago outlets. As in the case of *Moxostoma erythrurum* of the previous group, utilization of the latter outlet would have required the fish to follow the retreating glacier quite closely. In view of the restricted distribution in Ontario of the species here concerned, with no apparent geological barriers to limit further northward dispersal, temperature requirements may again be suggested as the inhibiting influence. If such be the case, these species most likely entered Ontario waters at a stage when the cold glacial waters had moved farther northeastward and only the Fort Wayne outlet to the Mississippi was available. The Lake Lundy stage would satisfy these requirements and also provide a wide channel into the Lake Ontario basin. Here again the proximity of the glacier may have kept these fish out of the Ontario basin until after the formation of Niagara Falls. The entrance of fish into the Lake Ontario drainage from Lake Erie in recent times through the Welland Canal is possible for species usually found in larger waters, but unlikely in the case of stream inhabitants such as *Microperca microperca*. Opinions differ as to the possibility of survival of the turbulence of Niagara Falls. There is, however, a third possible solution. The upper tributaries of the Grand River which drains into the eastern end of Lake Erie, and in whose watershed many of the species concerned occur, lie close to the headwaters of some of the streams draining into the west end of Lake Ontario. It is not improbable that at some earlier period, the cutting back of these headwaters caused them to mingle, so that fishes occurring in the upper Grand River system could cross over into the Ontario drainage and thence eastward.

While none of the species of this group has been recorded from the Lake of the Woods region of Ontario, most of them occur in Minnesota and some extend into North Dakota and Montana. As in the previous group, this suggests a limit of range at a more northern latitude in the west than in the east. Here again our knowledge of the northern limit

of range other than in Ontario and Wisconsin is extremely small. However, on mapping the most northern records in these two areas, there appears to be a definite relationship to the position of the 70° isotherm (fig. 23). In both Ontario and Wisconsin the points mapped lie,

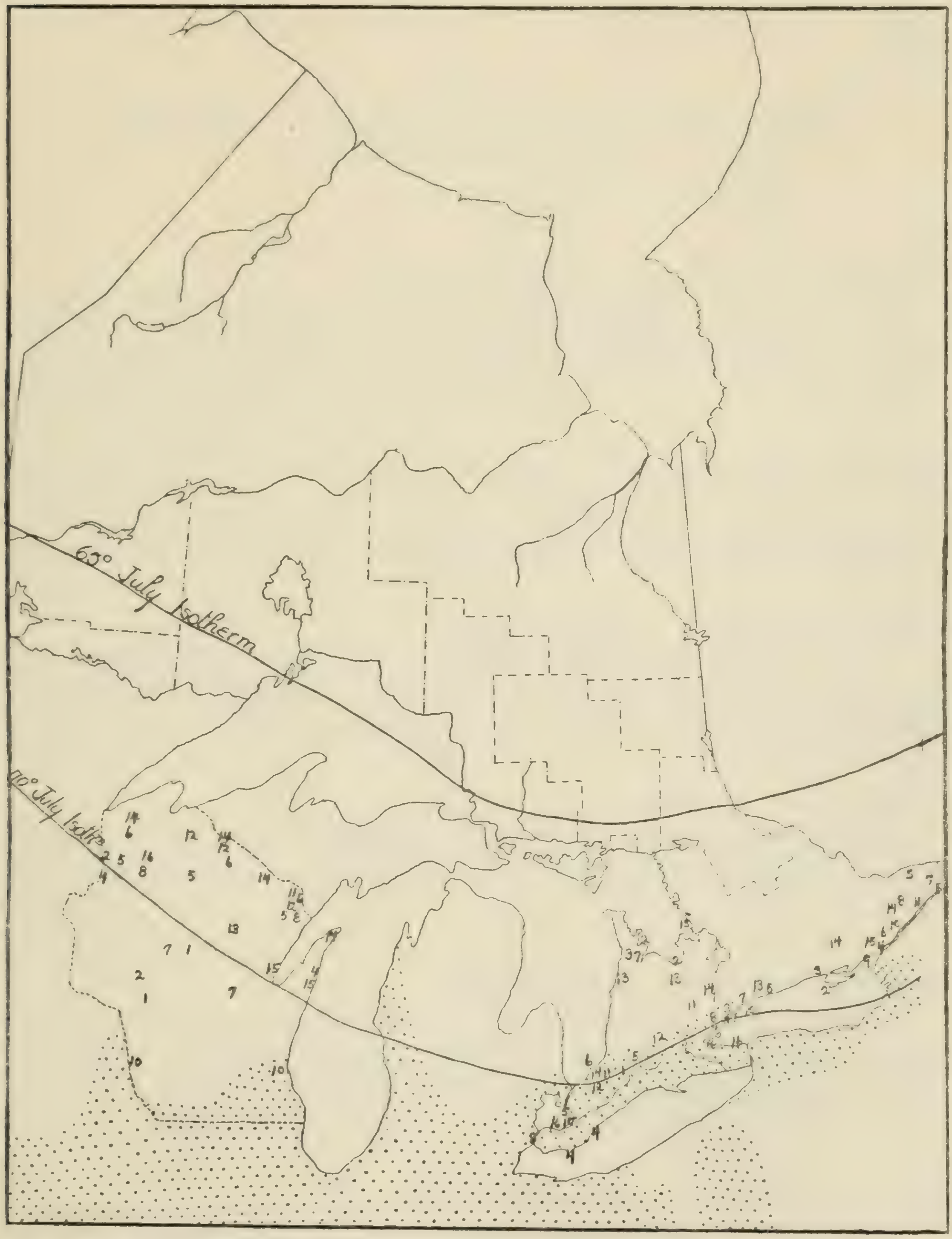


Figure 23. Distributional map showing the northern limits of range of the species of Figure 22, in Ontario and Wisconsin, in relation to the Carolinian Area (stippled) and the 70° and 65° July isotherms.

for the most part, in a strip of territory just north of the isotherm. This evidence supports the hypothesis based on the relationship of the range limits of the previous group to the isotherm, that temperature is the chief factor preventing certain species from dispersing farther northward when no geological barriers are present. In this instance, the required summer maximum is somewhat lower than for the group discussed earlier.

SPECIES OCCURRING MORE GENERALLY THROUGH SOUTHERN ONTARIO

Fig. 24 (p. 65)

Lepisosteus osseus. Long-nose gar.

Range: From North Dakota, Minnesota, Lake Huron, Lake Nipissing and Ottawa to Lake Champlain southward in the Atlantic coastal plain to Florida and in the Mississippi Valley to northern Mexico and Alabama.

Notropis heterodon. Black-chin shiner.

Range: From North Dakota through southern Ontario to Quebec, southward to Iowa, Indiana, Ohio and New York; in clear, weedy lakes.

Ictalurus lacustris. Channel catfish.

Range: From the Prairie Provinces to the Great Lakes and Ottawa-St. Lawrence basins, southward west of the Appalachians to northern Mexico and Florida; in lakes and larger rivers.

Umbra limi. Mudminnow.

Range: From Minnesota through southern Ontario to Quebec and Lake Champlain, southward to Iowa and Ohio; in pools and small streams.

Fundulus diaphanus. Banded killifish.

Range: From the Maritime Provinces through the St. Lawrence Valley and southern Ontario to North Dakota, southward on the Atlantic slope to North Carolina and in the Mississippi Valley to Iowa and Ohio; in shallow quiet waters.

Lepibema chrysops. White bass.

Range: From northwestern New York through southern Ontario and Michigan to Minnesota southward in the Mississippi Valley to Alabama and Texas; in the larger rivers and lakes.

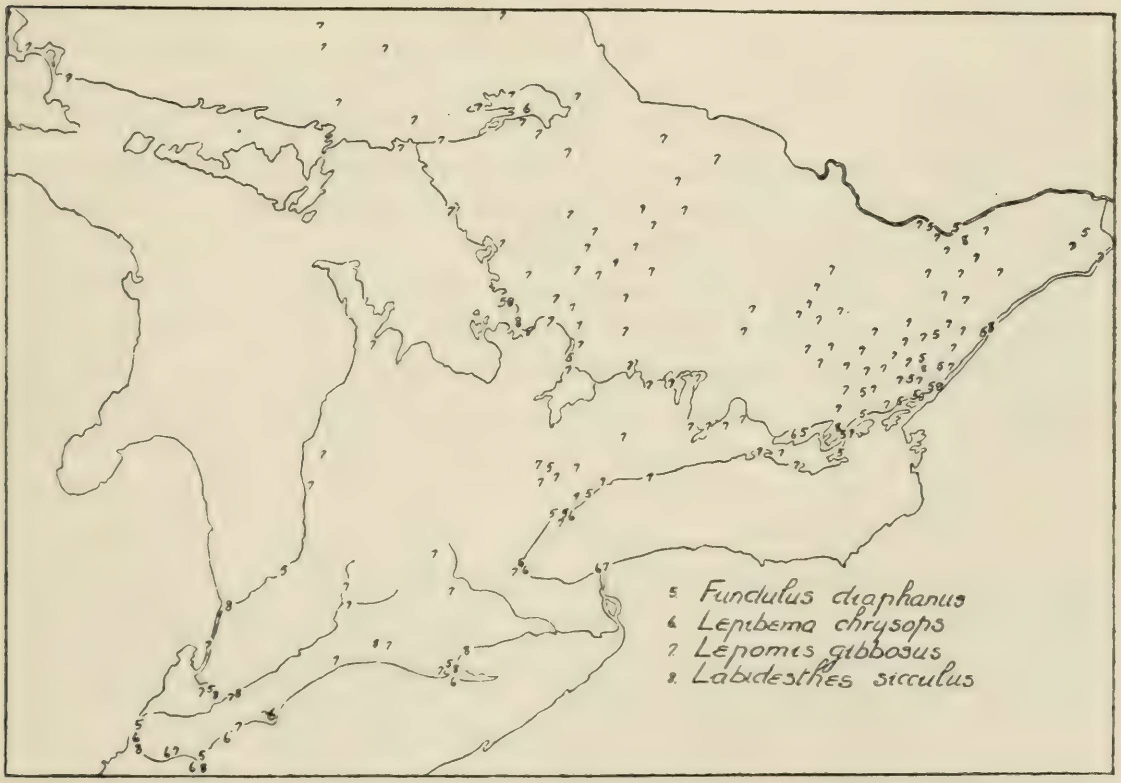


Figure 24. Species occurring more generally through southern Ontario.

Lepomis gibbosus. Pumpkinseed.

Range: From North Dakota through central Ontario to the Maritime Provinces, southward in the Atlantic coastal plain to Georgia, and in the Mississippi Valley to Pennsylvania and Missouri; in weedy lakes, ponds and streams.

Labidesthes sicculus. Brook silverside.

Range: From Minnesota through southern Ontario to northwestern New York and northern Pennsylvania, southward to the Gulf States; in surface waters of lakes and quieter parts of streams.

Of the species listed above (fig. 24, p. 65) *Fundulus diaphanus* and possibly *Lepomis gibbosus* appear to have entered Ontario from the Atlantic coastal plain as well as from the Mississippi Valley. Two subspecies of *F. diaphanus* occur in Ontario waters, *F. d. diaphanus*, the eastern form in the St. Lawrence and Lake Ontario basins, and *F. d. menona*, the western form in southwestern Ontario and the western end of Lake Ontario. The Mohawk-Hudson, Fort-Wayne and possibly the Champlain and Chicago were probably the outlets used in entering Ontario.

The fact that *oxyurus* is the only subspecies of *L. osseus* found in this province indicates that the population of this species came from the Mississippi Valley. Since the remaining five species are restricted in their eastward occurrence they too have probably been derived from only the Mississippi centre, entering Ontario by means of the Fort Wayne and perhaps the Chicago outlets.

Only one species, *Ictalurus lacustris*, appears to have reached the divide in time to make use of the Agassiz outlet. This fish has been recorded from Pine Island Lake, Saskatchewan, and other lakes through which the Saskatchewan flows, (*Silurus* (*Pimelodus*) *borealis*, Richardson, 1936) and from the Red River at Winnipeg (*Ictalurus punctatus*, Eigenmann, 1895). The other seven species occur through the upper waters of the Mississippi Valley but evidently reached the divide after the Agassiz outlet had ceased to exist. The northern limits of these fish in Ontario as seen in the accompanying maps reach various levels in the southern part of the province. It is difficult to say whether the apparent northern limit of those species found north of Lake Nipissing is the true one, since so little is known of the fishes between this region and the Lake Abitibi waters. However, none of the species of this group have been recorded from either the Abitibi or the Nipigon region where careful collecting has been done. Geological barriers may be responsible for restricting the more widely ranging species such as *L. gibbosus* but it

seems more likely that ecological factors have been more important. Temperature again seems the most likely influence, although in the case of *L. osseus*, *L. chrysops* and *L. sicculus*, which have been found only in the larger bodies of water, general habitat requirements may have kept them from penetrating into northern rivers and lakes.

SPECIES WHICH OCCUR IN THE LAKE OF THE WOODS AREA, ALTHOUGH OF RESTRICTED DISTRIBUTION IN SOUTHERN ONTARIO

Fig. 25 (p. 68)

The following five species are provisionally regarded as belonging to a different category from that of any of the others because they have been recorded, so far as Ontario is concerned, from the Lake of the Woods while occurring elsewhere in the province only quite far to the south. Since the section was written and the maps drawn Dr. Hubbs has informed us that examination of the two collections from Lake of the Woods identified by Evermann and Latimer (1910) as *Notropis umbratilis* proved them to be *Hyborhynchus notatus* and *Notropis cornutus frontalis* respectively. Similarly *Catostomus commersonnii* had been misidentified as *Hypentelium nigricans* and *Ameiurus nebulosus* as *A. melas*.

Hypentelium nigricans. Hog sucker.

Range: From Minnesota and southern Ontario, southward in the Mississippi drainage to Arkansas, and southeast through New York along the Atlantic coastal plain to Georgia. Since the Lake of the Woods record proves to be an error (see above) the most northerly records are those of Eddy and Surber (1943) "in the upper Mississippi near Wolf Lake, in Green Lake in Kandiyohi County, in the Kettle River and smaller tributaries of the St. Croix in Pine County" (Minnesota). It is found on the riffles of clear streams.

Moxostoma rubreques. Greater redhorse.

Range: From Lake Champlain and the upper St. Lawrence valley through the Great Lakes basin to Lake of the Woods, southward in the waters of the upper Mississippi drainage from Minnesota and Pennsylvania to Illinois and Tennessee; in lakes and clear rivers.

The record of the occurrence of this species in the Lake of the Woods requires more confirmation before final acceptance. Hubbs and Lagler (1941) state that its occurrence in the Ohio drainage of Pennsylvania and Tennessee is doubtful.

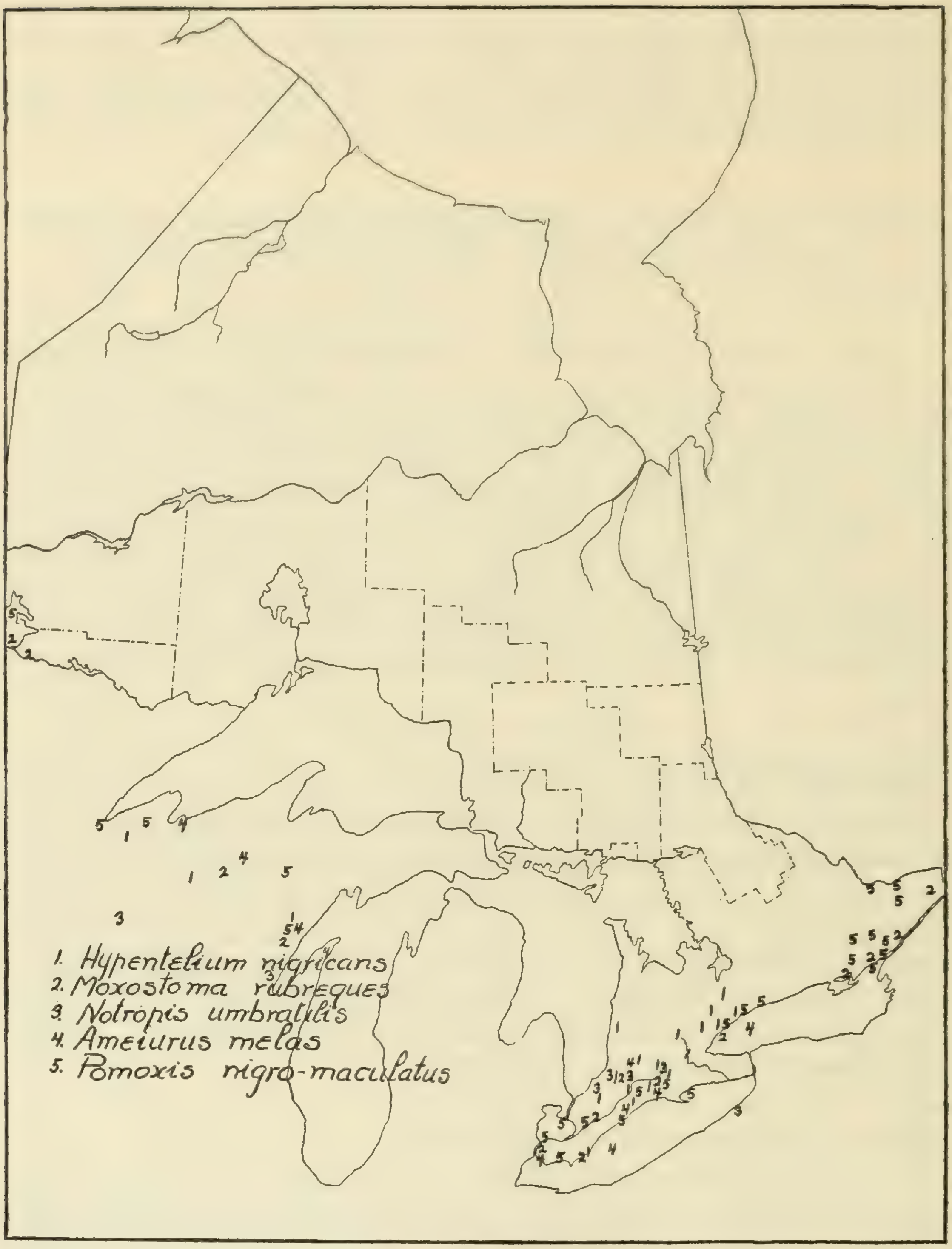


Figure 25. Species which occur in the Lake of the Woods area, although of restricted distribution in southern Ontario.

Notropis umbratilis. Red-fin shiner.

Range: Since the record of this species from the Lake of the Woods must be given up (see above) the known range is from northern New York through the Lake Erie basin westward to southern Minnesota, southward on the Atlantic coast to North Carolina, and in the Mississippi Valley to Alabama and Kansas; in lowland streams. The Ontario form is *N. u. cyanocephalus*.

Ameiurus melas. Black bullhead.

Range: From northern New York and southern Ontario to North Dakota, southward to Tennessee and Texas; in ponds and sluggish creeks. Evermann and Latimer's (1910) record from the Lake of the Woods was based on a misidentification (see above).

Pomoxis nigro-maculatus. Black crappie.

Range: From Minnesota and the Lake of the Woods to southern Ontario and Lake Champlain, southward in the Gulf drainage to Texas and Florida, north on the Atlantic slope to North Carolina; in weedy lakes, ponds and streams.

Of the above five species *Hypentelium nigricans* occurs well to the south in both the Mississippi Valley and the Atlantic coast region and may owe its post-glacial dispersal to both these centres, by utilization of the Agassiz, Mohawk-Hudson, Fort Wayne and perhaps the Chicago outlets. The three species, *Moxostoma rubreques*, *Ameiurus melas*, and *Pomoxis nigro-maculatus* have a restricted eastern distribution and appear to have come only from the Mississippi Valley, utilizing only the Agassiz, Fort Wayne and possibly the Chicago outlets.

The Ontario distribution of several of these fish, except for the possible occurrence in the Lake of the Woods region is similar to that of the species making up the preceding group. The presence in the Lake of the Woods region of fish which are otherwise quite restricted in their Ontario occurrence, although many other species of similarly restricted range have not been recorded from the Lake of the Woods, does not necessarily conflict with our conclusions regarding the relation of limit of range to the position of the July isotherm. The species so distributed conform with the type of range exhibited in the preceding group, as seen by their limits both in southern Ontario and in Wisconsin. Their occurrence in the Lake of the Woods would be quite understandable, on the basis of their relation to the 70° isotherm.

The revision in the distribution of *Notropis umbratilis* as suggested by Dr. Hubbs, restricts the Ontario occurrence of this species to the

extreme southwestern part of southern Ontario, i.e., the Lake Erie drainage. This species must therefore be regarded as belonging in that group whose distribution in Ontario is the most limited. According to the total range of this fish the Ontario occurrence is probably due to re-dispersal from an Atlantic coastal centre as well as from the Mississippi Valley.

SPECIES WHOSE ONTARIO DISTRIBUTION SUGGESTS FURTHER APPLICATION OF THE ISOTHERM THEORY

Figs. 26, 27 (pp. 71, 72)

Ichthyomyzon unicuspis. Silver lamprey.

Range: The St. Lawrence drainage from Quebec and Lake Champlain to Lake Ontario, lakes Erie, Huron, Michigan and Superior and reported from the Lake of the Woods, through the upper Mississippi waters as far south as St. Louis; in lakes and larger streams.

The silver lamprey is absent from most of the Lake Ontario waters. This is believed to be due to competition with landlocked members of the marine species of lamprey, *Petromyzon marinus*, (Hubbs and Trautman, 1937). The distribution of *I. unicuspis* in Ontario appears to have been produced by dispersal through all the glacial outlets connected directly with the Mississippi Valley, i.e. the Agassiz, St. Croix, Chicago and Fort Wayne outlets.

Amia calva. Bowfin.

Range: From the St. Lawrence drainage through the Great Lakes to Minnesota, southward in the Gulf drainage to Texas and Florida and north in the Atlantic coastal plain to the Carolinas; in lakes and sluggish rivers.

Moxostoma anisurum. Silver redhorse.

Range: From Lake Champlain and the upper St. Lawrence basin northwest to the Hudson Bay drainage in Manitoba and southward west of the Appalachian Mountains to Alabama and Missouri; in lakes and large rivers.

Chrosomus eos. Northern red-belly dace.

Range: From northern British Columbia and the Hudson Bay drainage of Canada east to New Brunswick, south to New Jersey and the Susquehanna system in Pennsylvania, through the Great Lakes and the Mississippi drainage from southern Michigan to Minnesota, the Dakotas and Colorado; in bog ponds and creeks.

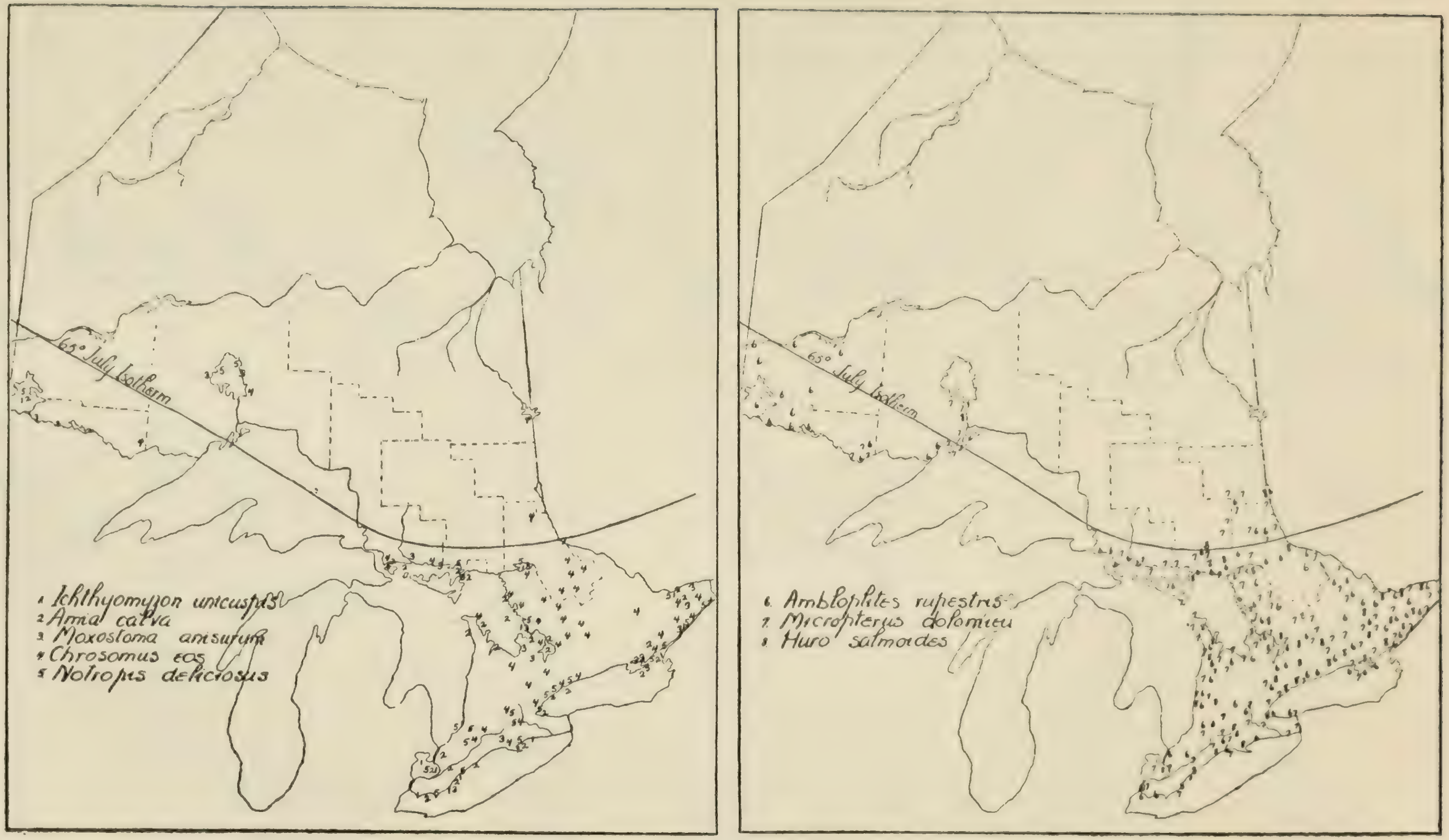
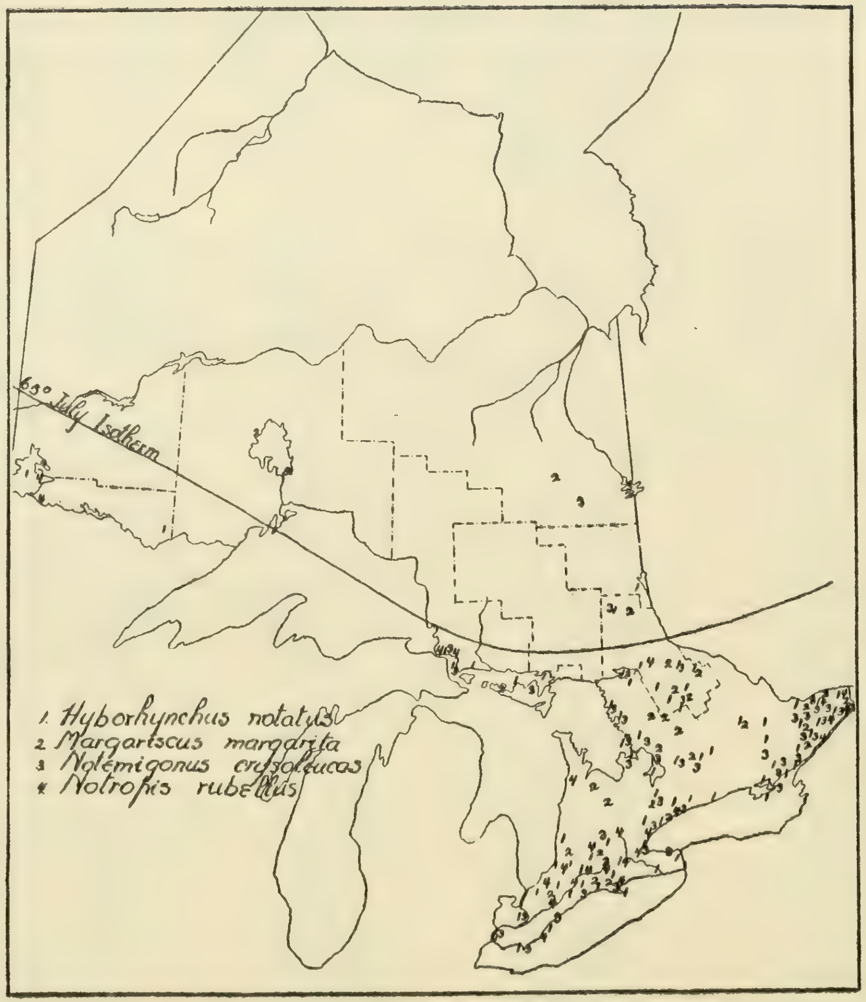


Figure 26. Species whose Ontario distribution suggests further application of the isotherm theory.



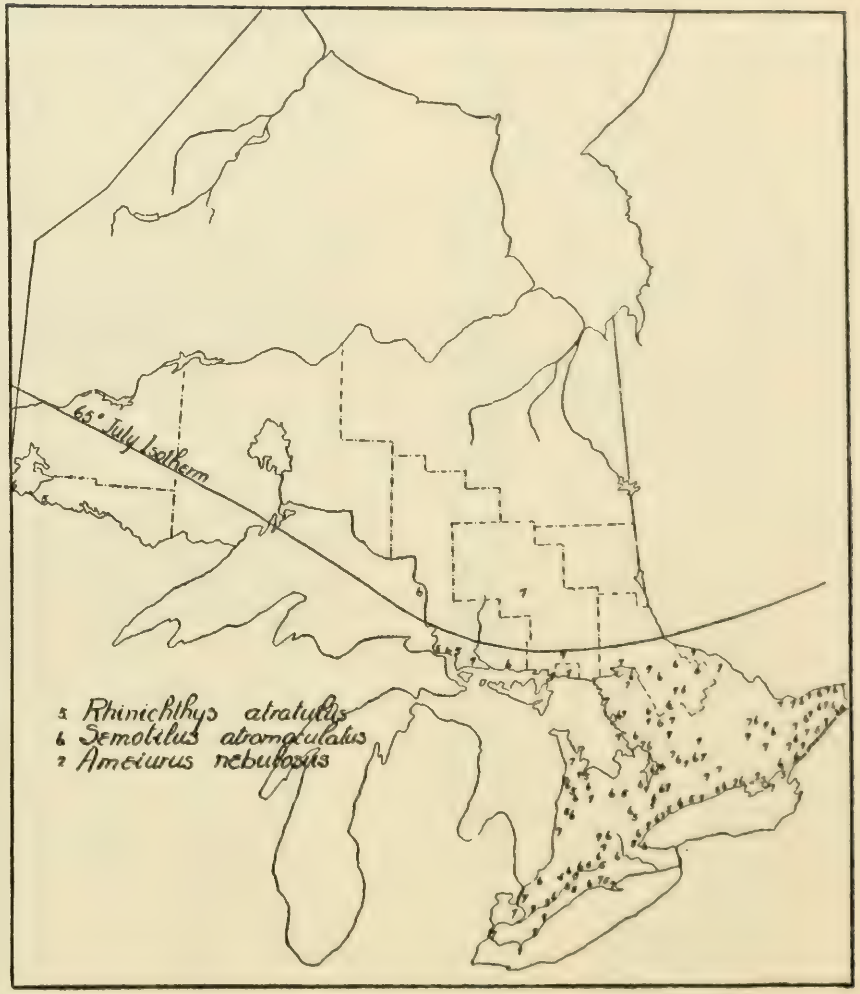


Figure 27. Species whose Ontario distribution suggests further application of the isotherm theory.

Hyborhynchus notatus. Blunt-nose minnow.

Range: From southern Quebec through the Atlantic coast drainage to Virginia, westward through the Great Lakes region to North Dakota and Winnipeg in southern Manitoba (Forbes and Richardson, 1920), southward to the Gulf states; in streams, lakes and ponds.

Margariscus margarita. Pearl dace.

Range: Southern Canada from the Maritime Provinces nearly to the Rocky Mountains, southward on the Atlantic slope to South Carolina, through northern Michigan, to Wisconsin, Minnesota and the Dakotas, also as relics in Nebraska; in cool lakes and creeks. The Ontario form is *M. m. nachtriebi*, the northern subspecies.

Notemigonus crysoleucas. Golden shiner.

Range: From Manitoba through the Great Lakes drainage of Ontario and the St. Lawrence region to New Brunswick, southward in the Atlantic coastal plain to Virginia and in the Mississippi Valley to Arkansas and the upper Ohio valley; in weedy lakes and quiet streams.

According to Hubbs and Lagler (1941) the western form *N. c. auratus* occupies most of Ontario except for the St. Lawrence basin and the eastern end of Lake Ontario where the typical (eastern) subspecies occurs, intergrading with *auratus*.

Notropis deliciosus. Sand shiner.

Range: From the Lake Champlain and upper St. Lawrence basins through southern Ontario to Lake of the Woods, southward to Tennessee and northeastern Mexico; in sandy lakes and larger streams. The Ontario form is *N. c. stramineus*, the northern subspecies.

Notropis rubellus. Rosy-face shiner.

Range: From Lake Champlain south to Virginia in the Atlantic coastal plain, westward through the Great Lakes to the Lake of the Woods and the Red River drainage of North Dakota, southward in the tributaries of the Ohio and upper Mississippi rivers to Missouri; in clear streams. Since the section was written Dr. Hubbs has determined that the reported occurrence of this species in the Lake of the Woods has been due to the erroneous identification of specimens of *Notropis atherinoides*.

Rhinichthys atratulus. Black-nose dace.

Range: From North Dakota and the Lake of the Woods through the Great Lakes basin to Quebec, southward on the Atlantic slope to Virginia and in the Mississippi drainage to Iowa and the Ohio Valley; in

cool streams. The Ontario population is *R. a. meleagris* except in the eastern end of Lake Ontario and the St. Lawrence basin.

Semotilus atromaculatus. Creek chub.

Range: Through the Atlantic coast drainage from the Gaspe Peninsula to Georgia, westward through the St. Lawrence and the Great Lakes basins to the Lake of the Woods, the Red River and Montana, southward in the Gulf drainage to New Mexico; chiefly in smaller rivers and streams.

Ameiurus nebulosus. Brown bullhead.

Range: From New Brunswick south in the coastal drainage to Virginia, westward through the Great Lakes drainage and northern part of the Ohio valley to North Dakota; common in ponds, streams and lakes. Introduced into some areas outside its natural range, e.g. British Columbia.

Ambloplites rupestris. Rock bass.

Range: From Manitoba to Lake Champlain, north in Ontario to Lake Abitibi, southward to Oklahoma and Alabama, and on the Atlantic slope to the Susquehanna (result of canals and introductions? Hubbs and Lagler 1941); in weedy and rocky lakes and streams. The Ontario form is *A. r. rupestris* the northern subspecies.

The majority of the preceding thirteen species appear to have been derived from the Atlantic centre of dispersal as well as from the Mississippi Valley, utilizing the Champlain, Mohawk-Hudson and all the Mississippi outlets. Four species, *Amia calva*, *Moxostoma anisurum*, *Chrosomus eos* and *Amboplites rupestris*, were probably derived from only the Mississippi centre. *A. calva* is represented in the Atlantic coastal drainage as far north as the Carolinas so that this centre has not been able to contribute to the Ontario population of this species. *A. rupestris* occurs on the Atlantic slope as far south as the Susquehanna but it is believed that this eastern occurrence is the result of dispersal by canals and introductions (Hubbs and Lagler, 1941). Utilization of the Agassiz outlet as established by the occurrence in the Lake of the Woods drainage is evident in all but two cases. *Margariscus margarita* and *Notemigonus crysoleucas* both occur in North Dakota, but have not been recorded from the Lake of the Woods basin. *N. crysoleucas* has been taken in the Red River drainage (Hankinson, 1929) and so has made use of the Agassiz outlet. It is quite possible that further collections in the Lake of the Woods area may extend our knowledge of the range of this species and perhaps of others.

Micropterus dolomieu. Small-mouth bass.

Range: The original distribution of this species included the watersheds of the Great Lakes, St. Lawrence River, and southward in the upper Mississippi, Ohio and Tennessee Rivers; in cool streams and clear lakes. The range has been considerably modified by introduction into various areas in which small-mouth bass were not native. One of these is the Lake of the Woods region where this species is now established. The utilization of the Erie Canal, opened about 1825, has enabled it to enter the Hudson valley and subsequent introduction has extended its range through the New England and Middle Atlantic States.

In Ontario the known native occurrences of small-mouth bass include southern Ontario, extending as far north as the waters just north of Lake Nipissing, as well as the region south of Lake Nipigon. This dispersal appears to have been developed through utilization of those glacial outlets which connect the Great Lakes with the Mississippi Valley. It is obvious that the Chicago and Fort Wayne outlets were utilized. The part played by the western outlets is not so evident. Although the records from the Lake of the Woods are known to be the result of introduction, the origin of the occurrence of *M. dolomieu* in Quetico Park, Rainy River District, (R.O.M.Z. questionnaire, 1937) is somewhat doubtful. Eddy and Surber (1943) say that originally the range of the small-mouth bass in Minnesota was virtually limited to the Mississippi drainage and that it is extremely doubtful that it occurred in the Red River drainage except where introduced. The Agassiz outlet does not appear to have been instrumental in aiding dispersal into Ontario waters and probably was not utilized at all by this species.

Huro salmoides. Large-mouth bass.

Range: From southern Ontario and southwestern Quebec through the Great Lakes system and Mississippi Valley to northeastern Mexico and Florida, north along the coastal plain to Virginia; in lakes and slow-moving rivers with an abundance of vegetation. Utilization of the Erie Canal and introductions into various waters have modified this range.

The original range of this species in Ontario is similar to that of the small-mouth bass, with certain local differences due to habitat preference. Here also the distribution is complicated by introductions and it is doubtful whether the record from the Nipigon River region (R.O.M.Z. questionnaire, 1935) represents a natural occurrence. At present the large-mouth bass also occurs in the Lake of the Woods area where it has been introduced.

The large-mouth bass ranges widely through the Red River system in North Dakota (Hankinson, 1929) as a result of passage through the

Agassiz outlet, but this channel has not contributed to the occurrence of the species in Ontario, or, as far as is known in Manitoba. If the Nipigon River record should prove to be a natural occurrence the St. Croix outlet has probably been utilized as in the case of the small-mouth bass in attaining this northerly point. The large-mouth bass occurs widely through the Minnesota and Wisconsin tributaries of Lake Superior. Otherwise the Ontario distribution of *H. salmoides* appears to have been brought about by dispersal from the Mississippi Valley through the Chicago and Maumee outlets.

The general distributional facts of the fishes listed above have been dealt with sufficiently in the previous discussion. There is one feature, common to all the members of the group, which requires special consideration. An examination of the accompanying maps shows that, although some of these species have been derived from both a Mississippi and an Atlantic centre of dispersal, and some from a Mississippi centre alone, all have attained approximately the same northern limit of occurrence in Ontario. It must be remembered at this point that our information with respect to the distribution of fishes in northern Ontario is extremely limited. However, the results of collections which do not record these species in the waters of the Hudson Bay slope, north of Lake Nipigon, as well as our more certain knowledge that the two game species *Micropterus dolomieu* and *Huro salmoides* are not native north of the limits indicated by the maps, lead us to believe that we are justified in accepting the northern limits shown as a reasonable approximation to the truth.

The distribution of these species seems to offer further evidence in support of the summer isotherm theory. In the case of most of the species of this group, the positions of the most northern records show the same tendency to occur farther north as they are traced westward as did those of the species restricted to the extreme south of the province. Here the points lie approximately in the path of the 65° isotherm. At present the meagre information available does not afford support of this view with respect to the regions east and west of Ontario as was possible for the 70° isotherm. We can only suggest that these species appear to be unable to exist in waters which do not attain a certain summer temperature. This is further supported by knowledge of the breeding habits and requirements of *M. dolomicu*. According to Hubbs and Bailey (1938) this species carries out nest building and spawning activities at temperatures of 59° to 65° F., and while, in the southern part of its range the small-mouth bass breeds as early as the last of April, farther north the breeding time is later, so that in Lake Nipissing it usually begins in June (Tester 1930) and in Georgian Bay is carried on into July (Doan, 1940).

SPECIES WHOSE OCCURRENCE IN ONTARIO SUPPORTS THE THEORY OF A CENTRE OF DISPERSAL IN THE ATLANTIC COASTAL PLAIN

Fig. 28 (p. 78)

Exoglossum maxillingua. Cutlips minnow.

Range: From Lake Ontario and the St. Lawrence River through Lake Champlain, Cayuga Lake and the Hudson River, southward in the Atlantic coast drainage to Virginia; in warm streams preferably with moderate current and gravel bottom.

In Ontario waters this species has been taken only in the St. Lawrence River at Ivy Lea below Gananoque (R.O.M.Z. collection). Evermann and Kendall (1902) record the taking of the cutlips minnows at Clayton and Ogdensburg, New York. The records of the surveys made by the the State of New York Conservation Department in the St. Lawrence and Lake Ontario drainage, record this species from all the areas examined as far west as the Genesee system draining into Lake Ontario (Greeley, 1926).

Leucosomus corporalis. Fallfish.

Range: From the drainage of Lake Ontario, the Ottawa and St. Lawrence rivers, southward east of the Alleghanies to the James River in Virginia, eastward to the Miramichi River in New Brunswick (Cox, 1893), and northward through the tributaries of Lake St. John in Quebec, across the divide into the James Bay watershed (Chambers, 1896) and into the Moose River in northern Ontario (Melville, 1914); in rock pools of swift streams and in clear lakes.

Notropis bifrenatus. Bridled shiner.

Range: From western New York and the St. Lawrence River to Maine and southward in the Atlantic drainage to Maryland; in ponds and near marshes in lakes.

For Ontario waters the records of this species are as follows: spring brook near Gananoque, Leeds County (R.O.M.Z. collection); Rideau Canal drainage, Brewer's Mills, Frontenac County (R.O.M.Z. collection); St. Lawrence River, Gananoque, Leeds County (Toner, 1937); Bay of Quinte, Prinyer's Cove, Prince Edward County (Hubbs and Brown, 1929).

It is elsewhere shown that certain species of fishes, such as the shad and smelt, whose natural occurrence in Ontario is restricted to the south-eastern waters of the province, owe this distribution to the marine invasion which followed the glacial period. The three species listed above are similarly limited to the eastern drainage areas of Ontario.

A comparison of the ranges of the three species reveals that while *Exoglossum maxillingua* and *Notropis bifrenatus* do not appear to occur north of the St. Lawrence River and its immediate vicinity, *Leucosomus corporalis* is commonly found in the Ottawa drainage of Algonquin Park and of other areas in Ontario and Quebec, and has also been recorded as

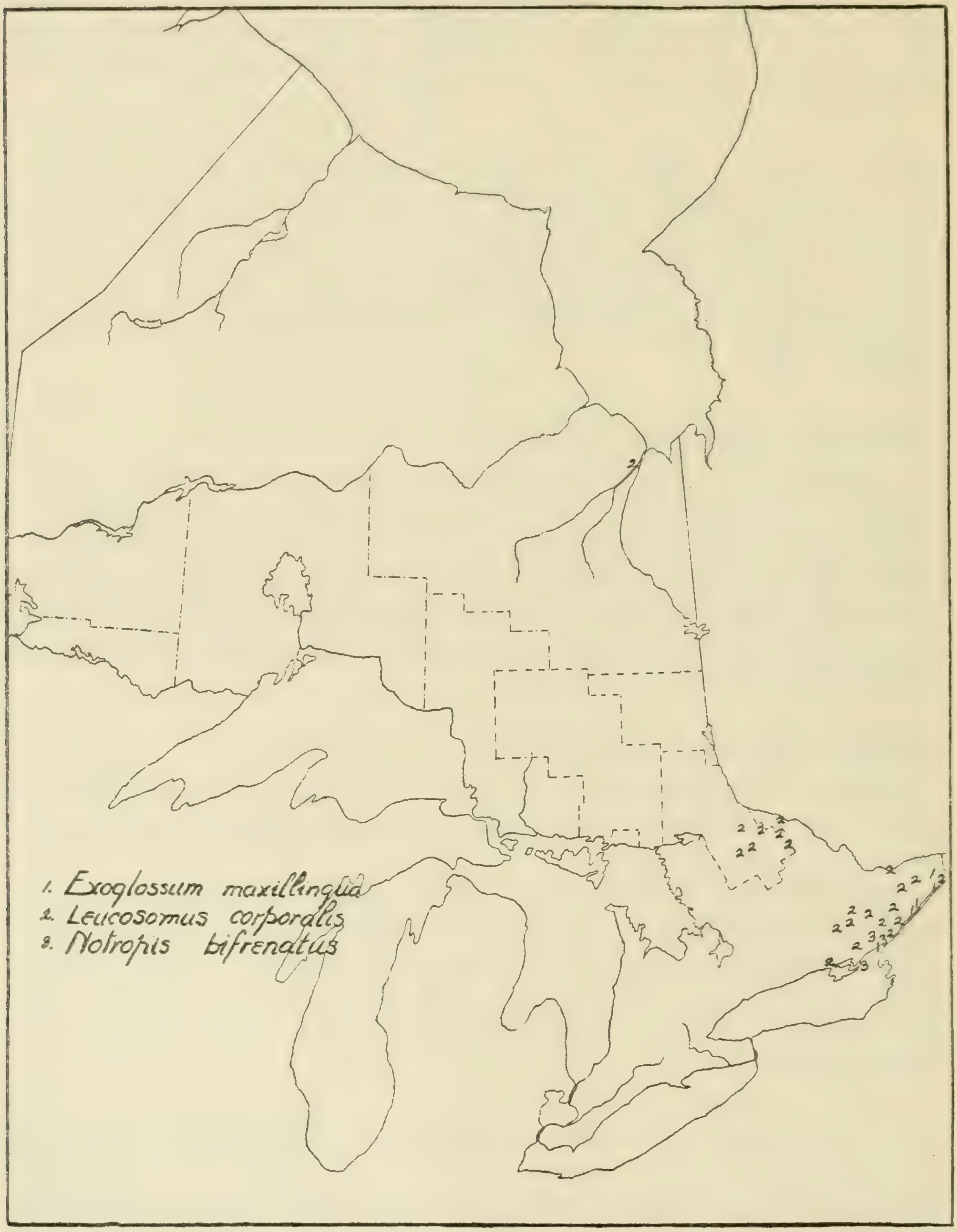


Figure 28. Species whose occurrence in Ontario supports the theory of a centre of dispersal in the Atlantic coastal plain.

far north as the Moose River. The southern parts of the ranges of the three species are, for the most part, similar. The most outstanding feature of the distribution of these species is that their ranges are definitely eastern and include no part of the Mississippi system. Since the ice sheet is believed to have completely covered the northern parts of the present ranges as far south as New York, it is evident that these fish must have survived the glacial period in the Atlantic coastal plain south of the edge of the glacier. As the ice retreated the glacial outlets formed in the development of the Great Lakes basins gave access to the more northern waters. By distributing themselves northward through these channels the three species under consideration have extended their ranges to the present limits.

The restricted occurrence of *E. maxillingua* and *N. bifrenatus* in the northern limits of their ranges leads to the conclusion that these two types have entered Ontario waters fairly recently. It may be that further dispersal is prevented by barriers of which nothing is known. In this event the present distribution represents the ultimate limit of the post-glacial dispersal. It is quite conceivable that further northward distribution may have been prevented by the temperature requirements of the species, but even if the lower temperature of more northern waters has prevented these forms from entering them there appear to be no geological barriers preventing dispersal eastward and westward along the shores of the St. Lawrence River and its tributaries. From this it is concluded that *E. maxillingua* and *N. bifrenatus* have entered Ontario waters fairly recently and their limited occurrence in this province is due to insufficient time for further dispersal. This view is supported by the fact that while the known distribution of the two species in Ontario consists of a few records from the north shore and tributaries of the St. Lawrence River, on the south or New York side there are a considerably larger number of records from the St. Lawrence and from the tributaries of Lake Ontario as far west as the Oswego system in the case of *N. bifrenatus* and the Genesee system in the case of *E. maxillingua.* The presence of these species in the New York tributaries of Lake Ontario may indicate utilization of the Mohawk-Hudson outlet. While this was active the ice front stood not far to the north of this region and it is not likely that these fish could exist in the cold waters which must have occupied the drainage channels. Also, if the cutlips minnow and bridled shiner entered the western New York tributaries via the Mohawk-Hudson outlet, they have had sufficient time to extend their ranges much further westward along Lake Ontario than the present limit of occurrence. The distribution of *E. maxillingua* and *N. bifrenatus* as it

now stands appears to be merely the existing phase of a process of dispersal which has by no means reached its limit. In the geological history of the Lake Ontario basin a post-glacial outlet is described which led from the eastern end of the basin into the Champlain watershed and from there into the Hudson valley. This outlet may have been responsible for the northward distribution of the species under consideration. The same objections arise here as in the case of the Mohawk-Hudson outlets. In the geological history it is suggested that at the maximum extent of the marine invasion a connection existed between the Atlantic Ocean in the New York region and the Champlain Sea through the Hudson valley. The species under discussion are definitely fresh-water forms and there is little possibility that their northward dispersal could have taken place through the Hudson valley during the time of this marine invasion. But it is not unlikely that when the sea receded, a fresh-water connection between the Lake Champlain and Hudson River watersheds again existed for a time and, at this stage representatives of *E. maxillingua* and *N. bifrenatus*, were probably able to move northward through the freshwater Hudson channel into the Lake Champlain region from which further dispersal carried them to the St. Lawrence and along the shores into its tributaries and those of Lake Ontario. The limited distribution of the species in the Ontario waters of the St. Lawrence as compared with that on the New York side is probably due to the deep swift waters of the river forming an effective barrier to northward dispersal. After reaching the St. Lawrence, dispersal eastward and westward in the New York waters could easily take place. At some later period, probably within recent times, representatives of these two species appear to have succeeded, perhaps at a low water stage of the river, in crossing to the north shore and in the case of *N. bifrenatus*, extending their range into a few tributaries in Ontario.

The most peculiar distributional problem of any Ontario species is presented by *L. corporalis*. As previously stated, the fallfish is believed to have survived the glacial period in the Atlantic coastal plain and made use of the eastern glacial outlets in the course of its redistribution northward. The present occurrence of the fallfish in eastern Ontario is probably the result of dispersal through the Mohawk-Hudson and Champlain outlets, while the restriction of this species in Ontario to the drainage of the Ottawa and upper St. Lawrence rivers and the eastern end of Lake Ontario may be attributed to habitat requirements. The fallfish is most often found in the rocky pools of clear, swift streams or in clear lakes. At spawning time in the spring, streams with smoothly-flowing water and gravel beds are required. The Ontario waters flowing

into Lake Ontario west of the area in which these fish are found drain a different type of country and provide different habitats from those of southeastern Ontario where outcrops of the Canadian shield are common. The record of *L. corporalis* from the Moose River in northern Ontario is not so easily explained since there is no evidence that the fallfish used the Temiskaming outlet of Lake Ojibway in order to reach the James Bay tributaries. For some time it was thought possible that members of this species might have passed northward along the coast of Labrador and thence west to Hudson and James Bays. Some support of the idea that the fallfish could travel through coastal waters was given by a record of this species from New York Harbour (Bean, 1903). However, the investigation of the range of the fallfish in Quebec has given rise to a more plausible theory. Chambers (1896) records the occurrence of *L. corporalis* in tributaries of Lake St. John, Quebec as well as in several lakes northwest of this region. These lakes include Big and Little Nekebau on the St. John side of the height of land and Obahtegooman on the Hudson Bay slope. It seems likely, therefore, that at some time after the retreat of the glacier there was a freshwater passage across the height of land between the Lake St. John and Hudson Bay watersheds in the Lake Nekebau region where at present the two drainage systems are in close proximity to each other. Such a passage appears to have been traversed by the fallfish and accounts for the records of this species from the James Bay tributaries farther north. It is quite possible that collections in the waters southeast of James Bay would provide further evidence for this belief.

Megapharynx valenciennesi. Recently Legendre (1942) has announced the rediscovery of a species of catostomid called *Catostomus carpio* by Cuvier and Valenciennes (1844). Jordan in 1886 pointed out that *Catostomus carpio* Rafinesque, an *Ictiobus*, had priority over *C. carpio* Cuvier and Valenciennes, a *Moxostoma*. The latter species, he said, having no synonyms may receive a new name, *Moxostoma valenciennesi*. Later Jordan and Evermann (1896) wrongly, as now appears, regarded *valenciennesi* as a synonym of *Moxostoma anisurum*. Cuvier and Valenciennes' type was said to have come from Lake Ontario. Legendre's four specimens all came from waters near the junction of the Ottawa and St. Lawrence rivers,—Saint Anne de Bellevue (1), Lake of the Two Mountains to the north of Île Perrot (1), and off Dorion in the County of Vaudreuil, P.Q. (2). The limited distribution of *Megapharynx* in the upper St. Lawrence waters suggests its derivation from the Atlantic coastal area.

SPECIES WHICH PRESENT INDIVIDUAL DISTRIBUTIONAL PROBLEMS

Fig. 29 (p. 83)

Polyodon spathula. Paddlefish.

Range: Through the Great Lakes basin and southward in the Mississippi Valley from New York, Pennsylvania and Montana to Texas, Mississippi and North Carolina; in the larger lowland streams.

There are few records of this species for Ontario and all are from the larger bodies of water. The occurrence of the paddlefish in Lake Helen on the Nipigon River is recorded by Prince (1899). Nash (1908) cites a record for Spanish River, Georgian Bay. Halkett (1906) and Nash (1908) both refer to a mounted specimen in the Fisheries Museum at Ottawa, taken in Lake Huron near Sarnia. Dymond (1922) quotes Jordan and Evermann (1908) as saying "a single specimen has been recorded from Lake Erie, which it doubtless reached through the Waubash and Erie Canal."

The presence of *Polyodon spathula* in the Nipigon River, at the north end of Lake Huron and in Lake Erie indicates a possible utilization of the St. Croix, Chicago and Fort Wayne outlets. It is not certain that the canals in the St. Mary's River, and connecting Lake Michigan and Lake Erie with the Mississippi Valley, acting in conjunction with a tendency of the species to range widely in all available large bodies of water, have not been responsible for the distribution of the paddlefish in the Great Lakes.

Amphiodon alosoides. Goldeye.

Range: From the Mackenzie River in the Northwest Territories southward through the Athabaska, Saskatchewan and Mississippi river systems to Oklahoma and Arkansas, eastward in the Abitibi region and in the Mississippi basin to Pennsylvania; chiefly in lowland streams.

Hiodon tergisus. Mooneye.

Range: From the St. Lawrence and Great Lakes basins north to James Bay, west to Manitoba and Saskatchewan, southward in the Mississippi Valley to Arkansas, Kentucky, Pennsylvania and western Maryland; in the open waters of large lakes and streams.

These two species are discussed together in view of the somewhat unique problem they present. The details of their total distribution have been dealt with by Kerswill (1937). The present work adds a few records to the known distribution in Ontario and extends the range of the goldeye into the English River, Lac Seul and the Eagle River.

From the general statement of their ranges, these species appear to have spread northward from the Mississippi centre of distribution. This general range might also lead us to assume a general occurrence of both species in Ontario waters. The records for Ontario do not agree with such an assumption. Although in certain parts of the Mississippi Valley and

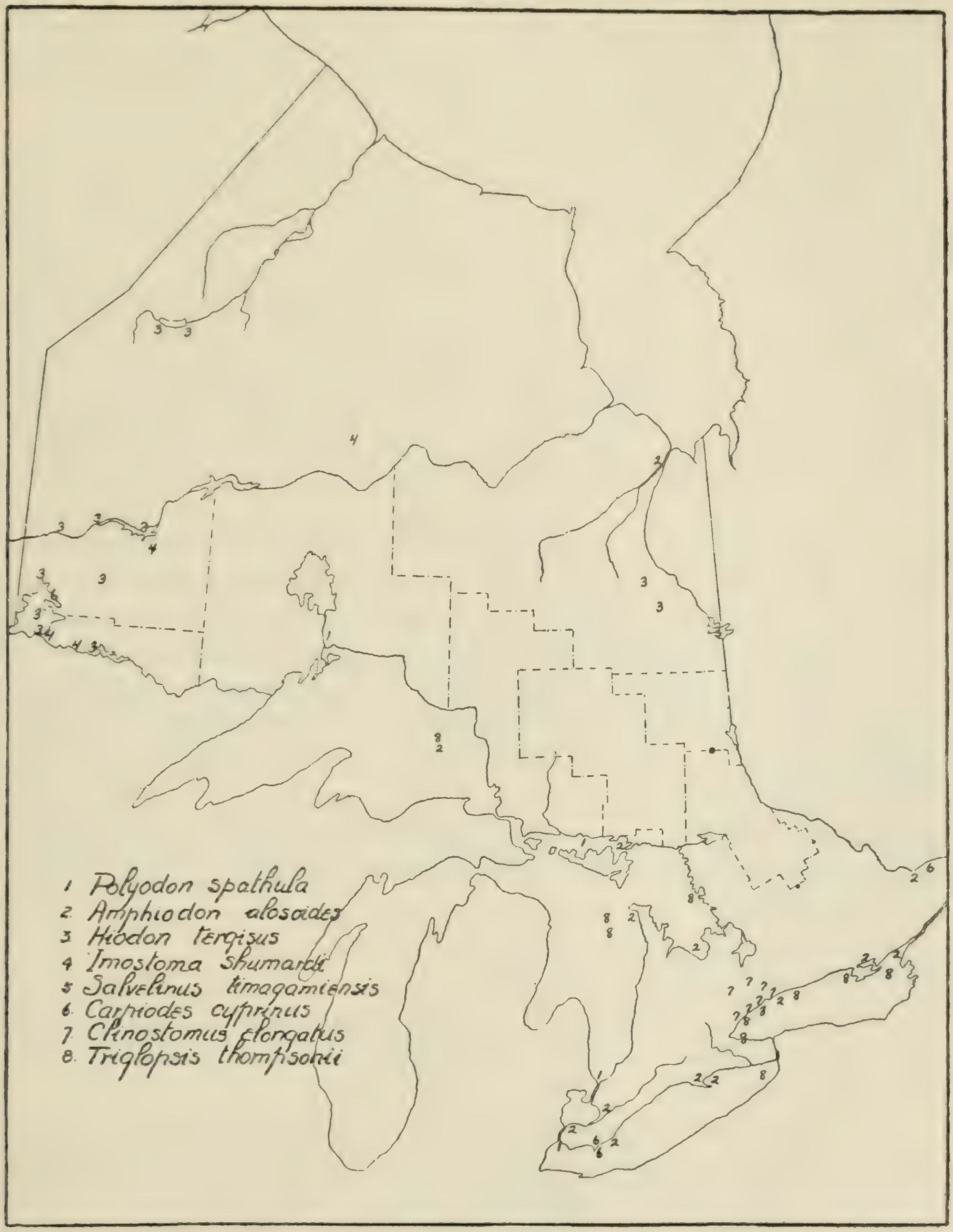


Figure 29. Species which present individual distributional problems.

the Western Provinces of Canada these two fish are found in the same waters, in Ontario they are not known to occur together. *A. alosoides* occurs in two separate populations, one in the Lake Abitibi area, the other from the Lake of the Woods area north to Sandy Lake. *H. tergisus* occurs more or less generally in southern Ontario and in the lower Moose River. This separation is most likely due to ecological factors since geological barriers do not appear to have restricted the northward dispersal. It seems probable that since they do occur together in certain parts of their ranges, the apparent separation in Ontario is due more to competition than to a preference for a particular habitat.

Not only does *A. alosoides* not occur generally in Ontario waters, but the records of distribution indicate two separate populations, one in the Lake Abitibi area, the other in the Lake of the Woods area, with the whole width of northern Ontario between them. The question of how the isolated Abitibi population came to be presents one of the most striking problems. According to Kerswill (1937), the occurrence of *A. alosoides* in Lake Abitibi may be the result of "journeying from Lake Winnipeg down the Nelson River to the southern part of Hudson Bay, then into James Bay and up the Abitibi River into Lake Abitibi." Although the Sandy Lake goldeyes might possibly have come by a similar roundabout path, they could more easily have entered from the Lake Agassiz basin. Such a solution for the Abitibi occurrence seems to expect too much of the ecological tolerance of the goldeye, and the desirability of finding evidence for a water connection across northern Ontario becomes apparent. As stated in the discussion of the post-glacial lakes, the limits of Lake Ojibway west of the Lake Nipigon area are uncertain. But it is known that the upper waters of the English and Albany Rivers lie close to each other in the northeastern corner of Kenora District.

At this point it may be well to introduce another species whose distribution in Ontario has some bearing on this water passage across northern Ontario.

Imostoma shumardi. River darter.

Range: From southern Manitoba and western Ontario through Wisconsin, Michigan and Ohio southward to eastern Oklahoma, Arkansas and Kentucky; in lakes and larger rivers.

The records of *I. shumardi* for Ontario to date are restricted to the western part of the province. Specimens in the Royal Ontario Museum of Zoology collection were taken at Sioux Lookout and Lake Attawapiskat. Evermann and Latimer (1910) record the river darter as *Hadropterus guntheri* from the mouth of Rainy River. It occurs ex-

tensively in the Red River of North Dakota (Hankinson, 1929) and has been taken at Winnipeg (Eigenmann, 1895). The Agassiz outlet is apparently the only glacial outlet which has assisted dispersal of this species into Ontario waters. Greene (1935) states that the occurrence of this species in the Lake Erie drainage indicates use of the Fort Wayne outlet and that either the Chicago outlet or the canal is responsible for the Lake Michigan occurrence. For some reason, perhaps ecological barriers, passage through these channels has not brought the river darter into the waters of southern Ontario.

The range of *I. shumardi* in Ontario may be broader than our information indicates, since this fish is said to occur in deep waters, areas not often reached by ordinary seining methods. However that may be, the significance of the three records for northwestern Ontario is obvious. Together with the available geological evidence, the presence of *A. alosoides* in the English River and in the Lake Abitibi area and the occurrence of *I. shumardi* in the upper English River and in Lake Attawapiskat leads to the conclusion that a water connection of some extent did exist between the western or Agassiz basin and the Lake Ojibway area and provided a passage through which fishes could distribute themselves eastward across the northern part of the province.

Salvelinus timagamiensis. Aurora trout.

Range: White Pine Lake in Gamble Township in the Temagami Forest Reserve (Henn and Rinkenbach, 1925).

This sole record of the existence of the Aurora trout has been the cause of much speculation as to the origin of this species. Undoubtedly this has occurred during postglacial times. Since *Salvelinus fontinalis*, the nearest relative of *S. timagamiensis*, is found in the same region as White Pine Lake and since the Aurora trout is found only in White Pine Lake, it seems reasonable to suggest that some fish of the *S. fontinalis* population became isolated in White Pine Lake when the retreat of the glacier and subsequent draining of Lake Ojibway gave place to the present watershed. The variability of many salmonoid fishes is well known but it is difficult to say here whether *S. timagamiensis* may be the result of mutation or of variation under certain conditions of environment.

Carpiodes cyprinus. Quillback.

Range: From the St. Lawrence drainage southward in the Atlantic coastal plain to Virginia; from southern Alberta and Manitoba through Minnesota and Iowa to Lake Huron and the Lake Erie drainage of

Ohio, Ottawa River, below Ottawa (Dymond 1939); southward to Tennessee and probably Arkansas in the Mississippi Valley; in lakes and the larger rivers.

Until recently the occurrence of the quillback in Ontario was believed to be limited to the Lake Erie and Lake of the Woods regions. This distribution appears to be the result of utilization of the Agassiz and Fort Wayne outlets, while records of this species from the Lake Michigan waters indicate that the Chicago outlet was also used. The quillback is apparently absent from the Lake Ontario basin since there are no records of its occurrence in either the Ontario or New York drainage of that lake. The nearest occurrence to Lake Ontario is that recorded for a tributary of the east end of Lake Erie (Greeley, 1928). From this it is concluded that this species entered the Lake Erie basin after the formation of Niagara Falls, and has not penetrated adjacent waters to any extent, although Nash (1908) states that the range includes Lake Huron. Wintemberg (1936) has recorded *Carpiodes* bones from a prehistoric village site in Grenville Co., Ontario.

Clinostomus elongatus. Red-side dace.

Range: Known at scattered points through the upper Mississippi Valley and lower Great Lakes drainage from Wisconsin and possibly Minnesota to New York and southward to the Susquehanna system; in clear streams.

The limited occurrence of *Clinostomus elongatus* in Ontario where it is found only in streams draining into the northwestern part of Lake Ontario, as well as its scattered occurrence throughout its range, are most likely due to the fact that this species is found only in clear streams. No doubt in earlier times, when more clear cool waters were available, the occurrence would be less disjointed. The easterly occurrence as far south as the Susquehanna system, indicates a likely Atlantic coast centre of dispersal while Iowa and Kentucky records suggest a Mississippi centre as well. Further dispersal northward beyond the present range has probably been prevented by some temperature requirement as in the case of other species discussed earlier in this work.

Triglopsis thompsonii. Deep-water sculpin.

Range: In deep waters of all the Great Lakes, also Lake Nipigon, and Torch Lake, Michigan.

The Ontario occurrence of this species includes lakes Nipigon, Superior, Huron, and Ontario, almost the total known range. Deep-water sculpins have also been taken in Lake Erie (Greeley, 1928). The origin of this limited distribution presents an unusual problem. Scharff (1911) in seeking biological evidence for explaining the distribution of

life in northeastern North America on the basis of a marine invasion from the Hudson Bay region rather than the effect of a glacial epoch, claimed the "marine relict" occurrence of *T. thompsonii* in the Great Lakes region as being highly significant. According to Scharff, sculpins of this species also occur in "tidal pools on the west coast of Hudson Bay." Similar instances of relict forms are known for Europe (Berg and Popov, 1932, Lonnberg, 1932a and 1932b). It is true that a similar type of sculpin (*Oncocottus quadricornis*) as well as several other closely related species, do occur in Arctic streams and in the Arctic Ocean (Greene, 1935), but whether *T. thompsonii* and *O. quadricornis* are identical has not yet been determined. It is possible that the deep-water sculpin became separated from its marine relatives and lived in the deep waters of northern North America before the onset of the last ice age. It is also possible that some of the Arctic sculpins were driven south by the glacier. In either case it seems likely that the cold waters at the foot of the glacier would provide suitable habitats in which these fish could survive the glacial period. As the glacier retreated the sculpins probably followed the ice closely in the streams and ponded waters and passed into the Great Lakes basins and into Lake Nipigon. It is likely that the sculpins occurred at some time in a great many of the waters which the glacier left in its retreat, but the removal of the ice and moderating climate resulted in suitable waters becoming rare so that the only surviving representatives are found at present in the Great Lakes area.

SPECIES WHOSE DISTRIBUTION IS BEST DISCUSSED IN RELATION TO SUBSPECIES

Fig. 30 (p. 88)

Hybognathus hankinsoni. Brassy minnow.

Range: From Lake Champlain and the upper St. Lawrence Valley through southern Ontario, westward to North Dakota, southward to Colorado, Iowa and northern New York; in streams and bog waters.

Hybognathus nuchalis. Silvery minnow.

Range: This species is represented by two subspecies of geographically separate ranges.

The typical subspecies, the western silvery minnow, is found through the upper Mississippi drainage from Montana to western Pennsylvania southward to Arkansas and Alabama; in pools and backwaters.

The eastern silvery minnow, *H. nuchalis regius*, occurs in the St. Lawrence and Ottawa drainages of Ontario, through the Lake Champlain and Connecticut River systems, southward in the Atlantic coastal plain to Georgia; in the larger streams and in lakes.

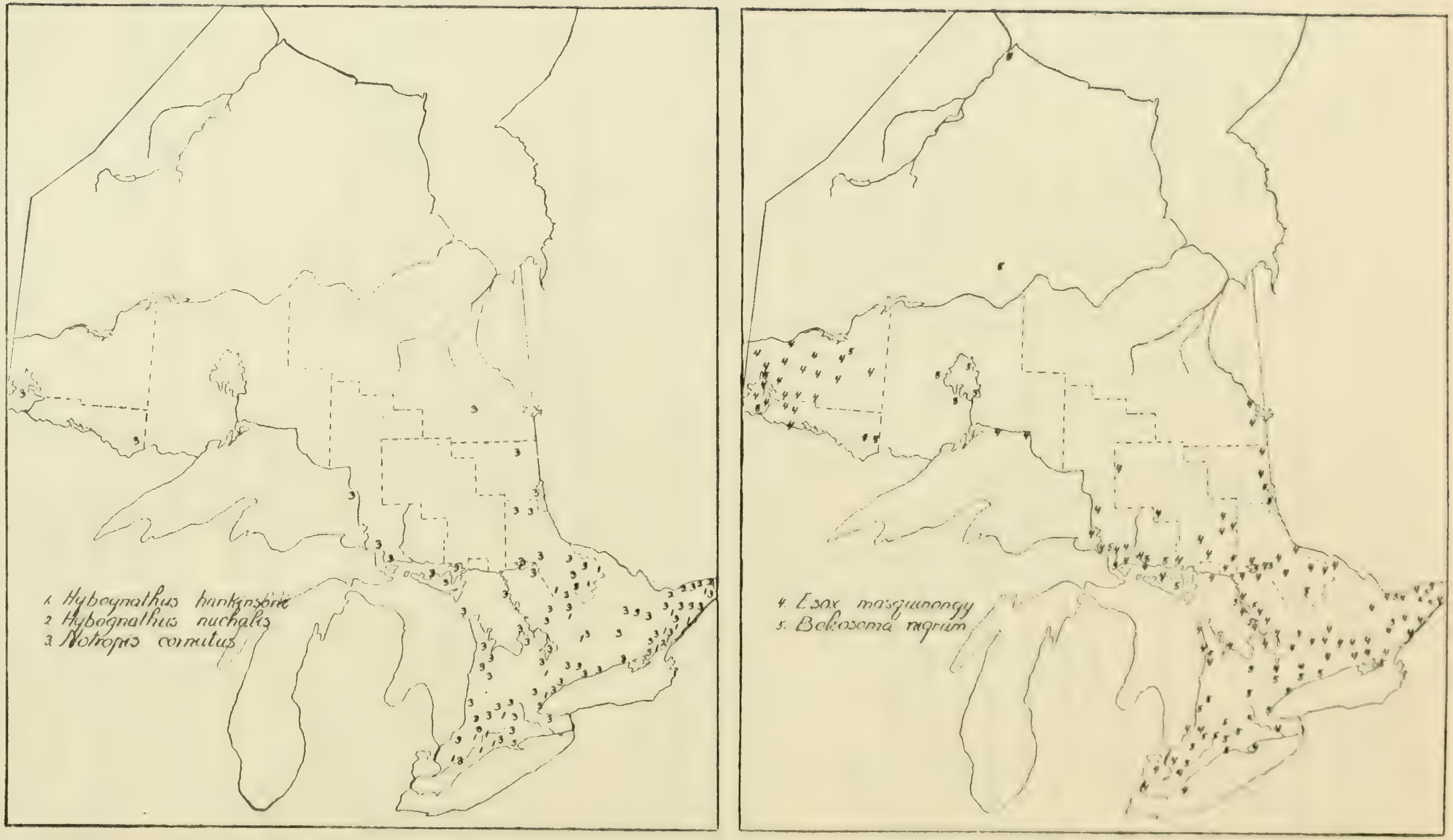


Figure 30. Species whose distribution is best discussed in relation to subspecies.

From the above outline of the general ranges and from the map, it is seen that while *Hybognathus hankinsoni* occurs throughout southern Ontario and the Mississippi Valley and is apparently of Mississippi derivation, the *Hybognathus nuchalis* population in Ontario occurs only in the eastern counties and has evidently been derived from the Atlantic coastal plain. Further dispersal of this species in Ontario is geologically possible but may be prevented by ecological barriers. It is quite likely that temperature conditions have prevented the spread of both species farther north.

It is difficult to say whether the restriction of *H. nuchalis regius* to the eastern tip of Ontario is due to habitat preference competition with *H. hankinsoni* or to insufficient time for further extension of range since glacial times. Dr. Hubbs doubts whether there is serious competition since *H. n. regius* is mostly in the larger rivers and lakes and *H. hankinsoni* in boggy ponds and creeks.

Notropis cornutus. Common shiner.

Range: From Saskatchewan to Quebec, southward in the Mississippi Valley to Colorado, Oklahoma and Alabama, and on the Atlantic slope to Virginia; in cool, clear streams and lakes.

The common shiner in so far as its general Ontario occurrence is concerned belongs among those species whose northern limits appear to have some relation to the 65° July isotherm. The general range of the species indicates two possible centres of post-glacial redistribution, in the Mississippi Valley, and in the Atlantic coastal plain.

Two subspecies of common shiner have been described: *Notropis cornutus frontalis*, the northern common shiner, ranges from Saskatchewan to Quebec, south to Kansas, Colorado, northern Illinois and Ohio, through Pennsylvania to northern New England. It occurs commonly through Ontario to the south of the 65° July isotherm.

Notropis cornutus chrysocephalus, the central common shiner, ranges from the southern parts of the Great Lakes, and the St. Lawrence drainage, east to Lake Champlain, south to Alabama, Arkansas and Oklahoma and is found in Ontario only in the drainage of lakes St. Clair, Erie and Ontario. Intergrades between the two subspecies occur where they inhabit the same waters. Sometimes segregation occurs where the Mississippi form is found usually in rivers and the northern form in creeks.

The northern form apparently had a Mississippi centre of redispersal. The northern limits of *N. c. chrysocephalus* in Ontario correspond to those of the group of fishes whose Ontario distribution is extremely limited and appears to bear some relation to the 70° July isotherm.

Esox masquinongy. Maskinonge.

Range: Lake Champlain, the St. Lawrence River and Great Lakes basin, north to Lake Abitibi, west to Lake of the Woods and south to Iowa and Illinois; to clear waters of the larger lakes and rivers.

Weed (1927) describes three species of maskinonge, two of which occur in Ontario waters. Other authors regard these as subspecies, as follows:

Esox masquinongy masquinongy. St. Lawrence maskinonge.

Range: Lakes Huron, Erie and Ontario, the St. Lawrence River, through the Lake Ontario and St. Lawrence River drainage of New York and Vermont north and east of Oswego, and in rivers and lakes of southeastern Ontario and southwestern Quebec.

Esox masquinongy ohioensis. Chautauqua maskinonge.

Range: The Ohio River basin from western New York to Alabama and North Carolina.

Esox masquinongy immaculatus. Northern maskinonge.

Range: The upper Mississippi Valley, through Wisconsin and Minnesota and northward.

From the above discussion it is apparent that the subspecies of *Esox masquinongy* which occur in Ontario are:

Esox masquinongy immaculatus in the Lake of the Woods region.

Esox masquinongy masquinongy from Lake Superior eastward. The exact limits of the ranges are unknown, although Weed (1927) considers that they do not overlap.

Weed (1927) suggests that before the last glacial period a uniform stock of maskinonge existed in the waters of the basins of the Great Lakes and the upper Mississippi Valley. As the ice sheet moved southward with the onset of the glacial period, the fish inhabitants were forced to move southward. In the west, the upper Mississippi was not covered by the glaciation and some of the fishes, including the ancestral maskinonge stock in that region, were able to remain in the "driftless area". Eastward, however, the ice lakes extended much farther south and the eastern representatives of the maskinonge species must have been forced to retreat southward out of the Great Lakes basins into the Ohio and lower Mississippi valleys.

During the maximum of the glacial invasions, the junction of the

Ohio River with the Mississippi waters from the northwest appears to have been blocked by ice so that communication between the maskinonge stock in the "driftless area" to the northwest and that in the Ohio and lower Mississippi tributaries was prevented. It was probably due to this isolation that differences began to arise which later produced the present subspecies.

The ice finally began to retreat. The northwestern element of maskinonge stock, which gave rise to *E. m. immaculatus*, was able to enter Lake Agassiz through the Minnesota and Warren rivers, and probably reached Lake Superior through the St. Croix outlet. Greene (1935) gives a distributional map which shows *E. m. immaculatus* in the upper Mississippi drainage of Wisconsin very close to the Superior divide.

In the Ohio valley, as the ice withdrew, some of the original stock which had been isolated in this area became adapted to the conditions there and remained in that region where they gave rise to the subspecies *ohioensis*. Others followed the ice northward, passed through the Fort Wayne and perhaps the Chicago outlets to the Great Lakes, where further isolation since the extinction of the post-glacial outlets may be held responsible for the development of the St. Lawrence maskinonge.

There is some possibility that the Great Lakes form, *E. m. masquinongy*, is a hybrid between the *ohioensis* and *immaculatus* subspecies, both of which seem to have had access to the Great Lakes basins. In connection with this suggestion Dr. Hubbs points out that *masquinongy* is the most distinct subspecies in colour pattern and believes that this fact is an argument against the hybridization theory.

Seaborn (1937) reports maskinonge of three colour patterns,—barred, spotted and green (largely devoid of dark markings) from the Sauble River which flows into Lake Huron at the base of Bruce Peninsula and suggests the possibility that some of these may be hybrids. Specimens of some of these in the collections of the Royal Ontario Museum of Zoology suggest hybrids between *masquinongy* and *lucius*.

Boleosoma nigrum. Johnny darter.

Hubbs (1926, 1928b, 1929, 1941) recognizes three northern subspecies of *B. nigrum* which are distributed as follows:

Boleosoma nigrum nigrum. Central Johnny darter.

Range: From Saskatchewan to Western Quebec, southward in the Mississippi Valley to Colorado, Oklahoma, Arkansas, Mississippi and Alabama (Related forms occur in the Atlantic drainage southward to the Carolinas). This subspecies occurs generally throughout Ontario

except in the extreme south where some habitats have been preempted by *B. n. olmstedi* and *B. n. eulepis*. In quiet sandy areas of lakes and streams.

Boleosoma nigrum olmstedi. Tessellated Johnny darter.

Range: From the drainage of eastern Lake Ontario to the Maritime Provinces, southward in the Atlantic coastal plain to North Carolina; probably intergrading with *B. n. nigrum.* In quiet waters and in stream riffles.

Boleosoma nigrum eulepis. Scaly Johnny darter.

Range: From the Lake Erie drainage of Ontario westward through Michigan to Wisconsin and Minnesota southward to Iowa, Illinois, Ohio and Pennsylvania, intergrading with *B. n. nigrum.* Commonly in weedier habitats than *B. n. nigrum.*

The distribution so outlined is probably explainable on the basis of three areas of redistribution. The three subspecies may have developed as the result of isolation during the glacial period. *B. n. olmstedi* evidently survived the glaciation in the Atlantic coastal plain. Because of its wide occurrence through the southern states, it may be concluded that *B. n. nigrum* survived in the Mississippi Valley and spread northward and eastward after the retreat of the glacier. *B. n. eulepis*, whose distribution is more limited, has probably been derived from the "driftless area". Restriction to a relatively small area has no doubt resulted in a narrowed tolerance of habitat, which, combined with competition from *B. n. nigrum*, an obviously more tolerant form, has permitted *B. n. eulepis* a relatively restricted dispersal. The northern limits of both *B. n. eulepis* and *B. n. olmstedi* in so far as they are known show some relation to the curve of the 70° July isotherm, although at this point any definite conclusion is impossible. Intergrades between *B. n. nigrum* and *B. n. eulepis* or *B. n. nigrum* and *B. n. olmstedi* may be explained as hybrids which have arisen during overlapping of the ranges of the subspecies.

SPECIES WHICH ARE OF MARINE DERIVATION

Fig. 31 (p. 93)

Petromyzon marinus. Sea lamprey.

Range: Atlantic coasts of Europe and North America as far south as Florida, ascending streams in the spring. Landlocked in Lake Ontario, Lake Champlain and in lakes of western and northern New York State; has recently spread to lakes Erie, Huron and Michigan.

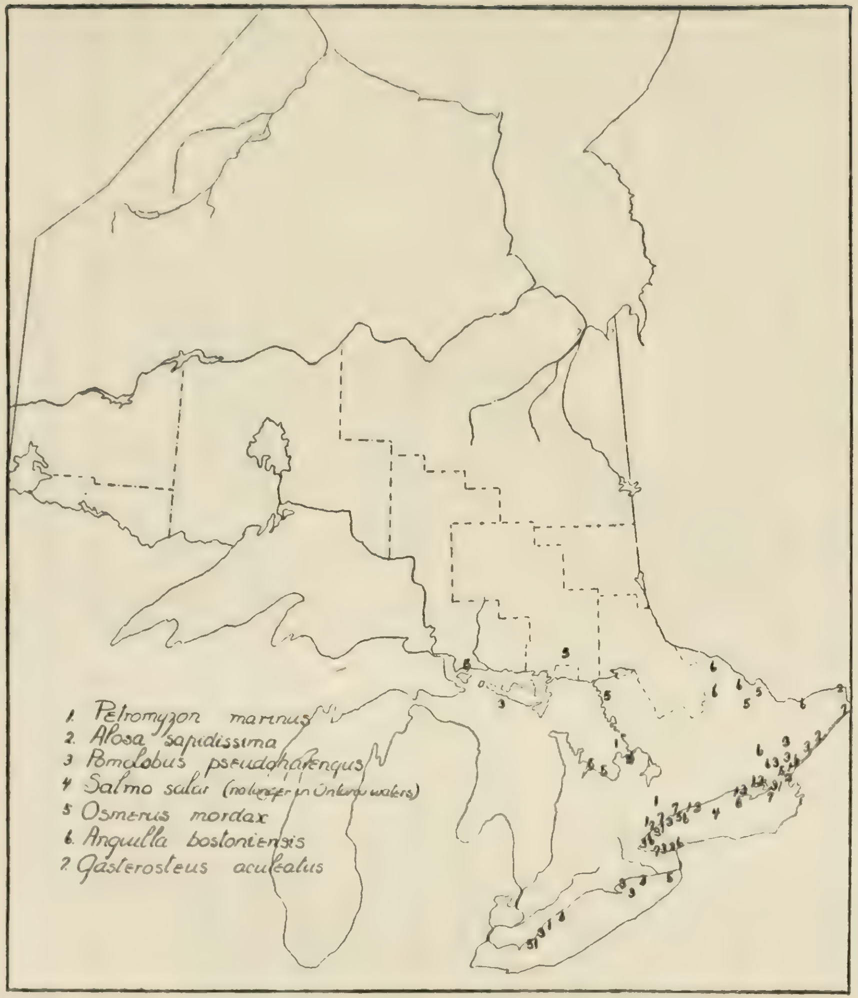


Figure 31. Distributional map of species whose occurrence in Ontario is of marine derivation.

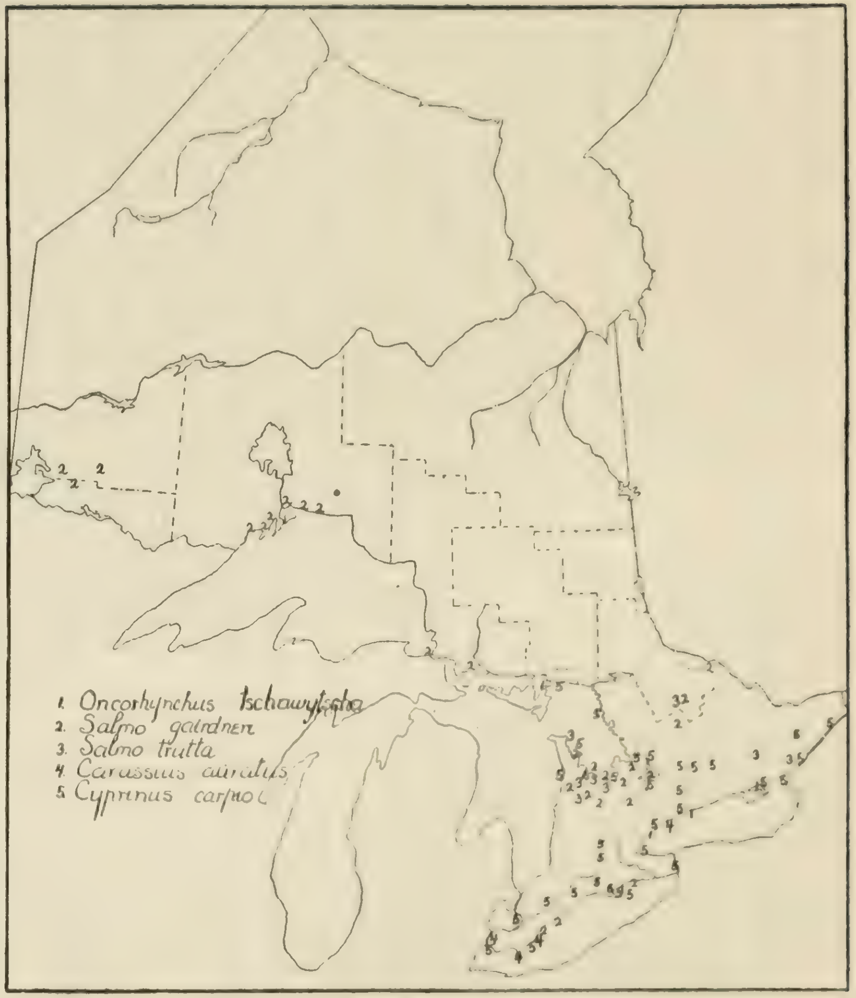


Figure 32. Distributional map of species which have been introduced into Ontario waters.

Although it is possible that lampreys migrate from the sea into the basins of the lower Great Lakes, most of the lampreys of this species occurring in Ontario are believed to spend their whole period of existence in fresh water. In 1915 Bensley included *Petromyzon marinus* provisionally in his "Fishes of Georgian Bay", on the reports of fishermen that lampreys fifteen inches long were sometimes taken on whitefish and trout from deep water. Since this species is typically marine and landlocked in areas concerned in the marine invasion, it is likely that its earliest access to Ontario waters was during the invasion of the Champlain Sea, rather than through the Hudson valley and Mohawk outlet. If this southeastern outlet had been used there was nothing during the early stages of existence of this passage, to prevent entrance into the Lake Erie basin through the Lake Lundy waters. On the other hand, if the sea lamprey entered the Ontario basin during the low or early marine stage, the Algonquin River was still in existence and would have given access to the Lake Huron basin. This might be assumed to account for the above-mentioned occurrence of the species in Georgian Bay. There seems no reason why the lamprey could not have distributed itself to Lake Erie by this route. Since the species was first recorded from Lake Erie in 1921 (Dymond 1922), when specimens were taken at Merlin, it seems likely that the sea lamprey entered the Lake Ontario basin after the Algonquin River had ceased to exist. The record for Georgian Bay, if true, (Bensley, 1915) must then be the result of recent distribution through the Trent Valley Canal system, or from Lake Erie, into which the lampreys came from Lake Ontario through the Welland Canal, previous dispersal in that direction having been prevented by Niagara Falls. Dr. Hubbs has recently (letter, September 28, 1943) informed us of the taking of a young *Petromyzon marinus* from a lake trout caught in Lake Huron off Kettle Point, Ontario, on May 22, 1943.

The absence of the sea lamprey from the Ottawa Valley, where *Ichthyomyzon unicuspis* is known to occur, is attributed to competition between the two species (Hubbs and Trautman, 1937). Perhaps the dam at Point Fortune has had some effect in preventing dispersal of the sea lamprey as it has in the case of the shad.

Alosa sapidissima. Shad.

Range: Atlantic coast of North America from New Brunswick to the Carolinas, ascending rivers in the spring to spawn.

In Ontario waters the shad at present occurs only in the lower Ottawa River. Wright (1892) considered that the shad "used to be abundant in the lower Ottawa River, but the pollution of the river by sawdust appears to have rendered its former spawning grounds unavailable". However, in 1937 several specimens were received at the Royal Ontario

Museum of Zoology from Point Fortune on the Ottawa River. MacDonald (1938) shows that while shad are prevented from going farther up the Ottawa River than Point Fortune by a dam with no fish ladders, they nevertheless still run in the Ottawa every spring, spawning on the sand banks in the river below the dam at Point Fortune or in the Lake of Two Mountains a few miles below. Dymond (1939) states "it is believed that some occasionally are able to ascend the Ottawa above Point Fortune."

Evermann and Kendall (1902) state that shad were planted in Lake Ontario in 1870, -71, -72, -77 and -78, only a few of which survived, and since 1885 few have been caught. Greeley and Bishop (1931) report the taking of a shad in Lake Ontario at Cape Vincent New York. In 1924, C. W. Nash obtained two shad off the mouth of the Niagara River (Dymond, Hart and Pritchard, 1929).

It seems likely that since shad run in the Ottawa River each spring, occasional specimens may stray into Lake Ontario and these may be responsible for the records of specimens taken in this region.

Pomolobus pseudo-harengus. Alewife.

Range: Atlantic coast of North America from Newfoundland to Florida, entering streams to spawn.

Jordan and Evermann (1896) state that the alewife occurs landlocked in lakes of western New York, and also in Lake Ontario where it is excessively abundant. Pritchard (1929) states that "there is some doubt as to when this species first appeared in the lake". Wright (1892) says that it was "introduced into Lake Ontario since 1873 and is now very abundant". It has been stated by a number of writers that the alewife was introduced through an error when the intention was to plant shad (*Alosa sapidissima*). According to fishermen at Bronte the alewife was very common in the late seventies.

Hubbs and Brown (1929) say "It would be interesting to determine why the alewife, the marine form of which is strongly migratory, should not have passed through the Welland Canal to populate Lake Erie". However, a few years later, Dymond (1932) records the taking of an alewife 7¾" long in Lake Erie in September 1931 by A. B. Hoover of Nanticoke. MacKay (1934) reports the taking of alewives in Lake Huron near Manitoulin Island in 1933. Van Oosten (1935) records alewives from Lake Michigan although it is thought that these may be the result of unintentional plantings rather than migrants from lakes Ontario and Erie.

The present distribution of *Pomolobus pseudo-harengus* in southwestern Ontario, is the result of dispersal through the Welland Canal to Lake Erie and thence through the Detroit River and Lake St. Clair to

Lake Huron. In time, distribution into Lake Michigan is quite probable and the canals in the St. Mary's River should allow access to Lake Superior, unless some ecological factor as temperature excludes it from the more northern latitudes.

The general opinion of the status of the distribution of the alewife favours the view that the species has been introduced into Lake Ontario. However, because the alewife is typically a marine form, although able to live successfully in fresh water, and because the invasion of the Champlain Sea is held responsible for the occurrence of other marine species, such as smelt and shad in certain eastern Ontario waters, it is not improbable that the presence of the alewife in Lake Ontario may also be attributed to the marine invasion. The presence of this species in some lakes in Frontenac and Leeds counties (Toner, 1934) is comparable to that of the smelt in Golden and Muskrat lakes near Pembroke, and supports the theory that the alewife may be a relic of the marine invasion. For that reason *P. pseudo-harengus* is included among the species grouped as marine derivatives.

Salmo salar. Atlantic salmon.

Range: North Atlantic waters, ascending suitable rivers in northern Europe and in North America from Cape Cod to Ungava Bay. Landlocked forms of this species are known in lakes of Maine, New Brunswick and Quebec.

In pioneer days the Atlantic salmon was abundant in the waters of the St. Lawrence region (Nash, 1908) and of Lake Ontario (Dymond, Hart and Pritchard, 1920) and is believed to have been plentiful in the Ottawa River (Small, 1883). It was previously believed that the Atlantic salmon began to use the streams of the Ontario region as spawning grounds at the time of the marine invasion, and, as the sea waters retreated, continued to migrate through the St. Lawrence River to carry out their breeding activities. However, Blair (1938) examined the scales of a salmon in the R.O.M.Z. collection, taken in Lake Ontario before 1870 and found no evidence that this salmon had ever been to sea. It is probable that the marine invasion was responsible for the entry of this species into Ontario waters and the descendants of the first migrants remained to carry on their life histories entirely in fresh water. Dispersal into Lake Erie and the Upper Great Lakes was prevented by Niagara Falls. The Atlantic salmon has been absent from Ontario waters for many years in spite of the efforts to restore it through hatchery methods (Annual Reports of the Department of Marine and Fisheries, 1870 etc.). The extinction of this species in Ontario waters is due chiefly to dams which barred the way to spawning grounds, deforestation and pollution.

Osmerus mordax. American smelt.

Range: Atlantic coast of North America from Virginia north to the Gulf of St. Lawrence, entering streams and often landlocked as in Lake Memphremagog and some small lakes in Ontario and Quebec. The smelt is also abundant in Lake Champlain.

The occurrence of the smelt in the upper Great Lakes is the result of introduction of this species in Crystal Lake, Michigan by the Michigan Conservation Department in 1906 and succeeding years (Creaser, 1925). Information on the spread of the smelt in the Great Lakes has been summarized by Van Oosten (1937a) and Dymond (1944). From the north shore of Lake Huron the smelt appears to have been dispersed southward along Georgian Bay and westward to Lake Superior. Another route for distribution has been around the south end of Lake Huron, north to Bruce Peninsula and Georgian Bay.

In the fall of 1936, a specimen of *Osmerus mordax* was received at the R.O.M.Z. from Port Crewe on Lake Erie. This first record from Lake Erie is believed due to dispersal from Lake Huron through the St. Clair and Detroit system.

In Lake Ontario, smelts have been taken at Bowmanville in 1931 and 1934. Whether these are migrants from Lake Erie through the Welland Canal, and thus derived from the Lake Michigan introductions, or whether they have come from the Finger Lakes introductions (Greene, 1935), through the St. Lawrence Valley from Lake Champlain or even from the sea has not been decided.

The smelt has been found landlocked in several lakes of the Ottawa valley. Specimens in the R.O.M.Z. collection were taken from Muskrat Lake and Golden Lake, Renfrew County, Ontario. Dymond (1937) refers to the similar occurrence of smelt in Quebec in Green Lake north of the Ottawa River and in Lac-des-Isles, 60 miles north of Ottawa in the Gatineau district. It is believed that these representatives of a typically marine species, occurring naturally in lakes so far inland, are relict forms, left in the area when the Champlain Sea, which stood over this part of Ontario and Quebec, retreated and the present system of lakes and rivers developed.

It is significant that marine beaches have been found at an altitude of 690 feet above sea level at Kingsmere near Ottawa. The altitudes of the lakes in which smelt are known to occur are as follows: Muskrat Lake 408 feet, Golden Lake 560 feet, Dorè Lake 468 feet, Lac-des-Isles about 530 feet, Green Lake 476 feet.

Anguilla bostoniensis. American eel.

Range: The North Atlantic waters from southern Greenland to Brazil, ascending all rivers and found throughout the Mississippi Valley; migrating to the sea for spawning.

The range of the eel in Ontario waters was originally limited almost entirely to the drainage of Lake Ontario, the St. Lawrence and the Ottawa River. Bensley (1915) reports the occasional taking of specimens at the mouth of the Severn River and at Waubaushene on Georgian Bay. Since this is the only record of its occurrence in the Lake Huron basin it is believed to be a recent migrant through the Kawartha and Trent valley system since the Trent Valley Canal was opened.

There are no definite records for the occurrence of eels in Lake Erie. Dymond (1922) quotes Osburn as saying that "according to Kirtland, the eel did not formerly inhabit the Lake Erie drainage, but if not, it has found its way there through the canals". Whether this access to Lake Erie has been attained through the canals across the divide from the Mississippi Valley or through the Welland Canal is not certain. Perhaps both have been utilized. Nash (1908) mentions the large numbers of young eels at the foot of Niagara Falls in summer, and it is quite probable that the migration of young eels coming from the sea into fresh water might easily carry them through the Welland Canal. In spite of the large numbers of young eels which could enter Lake Erie in this way, and possibly through the Ohio canals as well, the eel population in the Lake Erie basin has certainly not attained significant proportions.

The natural absence of eels from Lake Erie, before man-made canals provided them with a means of access, may be attributed to the peculiar features of the life history of the species. For most of its life the eel is a freshwater fish, descending to the sea to spawn. The adults die after spawning and not until the second spring do the young find their way to the rivers where they remain until full grown when they, in turn, go down to the sea to spawn.

Eels have lived successfully in Lake Erie while the post-glacial outlets allowed them to escape to the sea when the time for their spawning arrived. There seems to be some connection between the salt water and the maturation of the sexual organs which do not mature until some weeks have been spent in the sea. For this reason, when the post-glacial connections with the Mississippi Valley (i.e. the Fort Wayne outlet) and the Lake Lundy-Mohawk valley outlet to the Atlantic ceased to exist, young eels were prevented, in the first instance by the land divide between the watersheds and in the second by the formation of Niagara Falls, from entering the Lake Erie basin. If adult eels were left in the lake at this time, their migration to the sea could take place only through Lake Huron and the Algonquin River. Final extinction of this outlet would cut off all direct communication with the sea and the species, unable to mature and spawn in fresh water became extinct in the Great Lakes above Niagara Falls.

The distribution of the eel is, in any event, a recent and recurrent phenomenon controlled by the peculiarities of the life history of the species, and extending only into those waters into which the young eels are able to migrate.

Gasterosteus aculeatus. Three-spine stickleback.

Range: North Atlantic coast of Europe and of North America from New Jersey to Greenland, both coasts of the North Pacific; also in fresh waters of these regions; chiefly in shore waters and creek mouths.

In Ontario the three-spine stickleback is limited to the shores of James Bay, the St. Lawrence River and the shores and lower courses of tributaries of Lake Ontario but the species is known to occur in Masham Creek (Dymond, 1939) a tributary of the Gatineau River, north of Ottawa. The occurrence of this "landlocked" colony places the three-spine stickleback in the same category as the smelt, namely, as a relic of the marine invasion.

SPECIES WHICH HAVE BEEN INTRODUCED INTO ONTARIO WATERS

Fig. 32 (p. 93)

Oncorhynchus tschawytscha. King salmon.

Range: Pacific coasts of North America and Asia from Behring Sea southward to California and northern China, ascending all large streams to spawn.

When the Atlantic salmon was approaching extinction in Lake Ontario, efforts were made to establish this species of Pacific salmon. The first plantings were made in 1874 and the last of which we have record in 1925. Between these dates, plantings were made in at least fifteen years in two periods, 1874-1881 and 1919-1925.

Following these introductions, partly grown and adult King salmon were taken on many occasions, but there is no evidence that any reproduction has taken place within the lake or in any of its tributaries. The species has persisted no longer than can be accounted for on the basis of the survival of fish artificially planted (Dymond, Hart and Pritchard, 1929). Davidson and Hutchinson's (1938) error in stating that Dymond, Hart and Pritchard "report the establishment of sea-run populations of chinook salmon in the St. John River, New Brunswick, and the Port Credit River, Ontario" has been corrected by Huntsman and Dymond (1940).

Salmo gairdneri. Rainbow trout.

Range: Pacific coast of North America from Alaska to California, ascending streams to spawn; widely introduced in eastern North America in cool lakes and streams.

Rainbow trout first gained entrance to the waters of Ontario through plantings made by the United States Fish Commission in streams tributary to Lake Superior in 1895. The report of the Commission for 1904 stated that "The latest reports from Lake Superior give information that the steelhead spawned last spring in nearly all the tributaries of the north shore of the lake". They still run in these streams in spring at spawning time.

Rainbows were planted in the Sydenham River in Grey County about 1904 by Mr. John Miller. The report of the United States Fish Commission for 1904 records "Rainbow trout to applicant, Owen Sound, 20,000 eggs". The first record of the taking of a rainbow in Lake Huron was in May, 1904, when a four pound specimen was taken off Duck Island, just south of Manitoulin. Whether it originated from the Lake Superior population or from the Sydenham River introduction is of course impossible to say.

The stocking of rainbow trout by the Ontario Department of Game and Fisheries began in 1918. In the intervening years, over two million have been placed in more than one hundred waters of the province.

The habit of the steelhead rainbow, the type generally stocked in Ontario waters, of leaving streams and going to lakes before they reach a foot in length has long been recognized. On reaching sexual maturity, they enter streams in spring on the approach of the spawning season and leave again soon after the completion of spawning. It is only in large rivers such as the St. Mary's that rainbow trout are normally found except during the first year or two of their lives or at spawning time. The Pine River, a tributary of the Nottawasaga, is one of the few rivers in which rainbow trout larger than a foot in length remain throughout the year. Rainbow trout have therefore survived in Ontario chiefly in large bodies of water such as Lake Superior, Georgian Bay and Lake Simcoe. The failure to survive in our northern inland lakes is rather surprising but unanimity of such failure is quite striking.

All of the specimens taken in Ontario waters that have been identified have been of the coarse-scaled steelhead type.

References in the literature include Dymond (1922, 1932); Hubbs and Brown (1929), Rawson (1930), and Toner (1933).

Salmo trutta. Brown trout.

Range: Northern and central Europe; widely introduced in America.

First plantings of brown trout by the Ontario Department of Game and Fisheries occurred in 1913, although vague references to earlier

plantings and migration from the United States have been published (Ont. Dept. Game and Fisheries Report, 1929).

Since their first introduction by the Government, approximately three million brown trout have been placed in nearly two hundred lakes and streams of Ontario. No report is available as to the survival or failure to survive in many of these waters but in general it may be said that brown trout have provided fishing in far more waters in southern agricultural Ontario than in the rockbound lakes and rapid streams of the north. Part of this difference may be only apparent, since it is universally admitted that the brown trout is a hard fish to catch, especially in lakes. Fish have been seen for years in some lakes, for example,—Big Clear Lake, Frontenac County,—but efforts to catch them have been largely unsuccessful. On the other hand, brown trout are taken every year, sometimes in considerable numbers, in certain parts of such streams as the Humber, Credit, Grand, Speed and Sydenham (Grey County), also in the Muskoka River. In the latter, specimens have been taken in both North and South branches, up to 5¾ pounds in weight, mostly at Muskoka Falls and Bracebridge Falls.

In southern Ontario the favourite habitat of the brown trout appears to be a pool or pond fed by a stream. In general, it may be said that in Ontario brown trout show a preference for the quiet, placid waters like those of their native home in England, France and Germany. There is no evidence as to whether the species propagates itself in any Ontario waters.

Carassius auratus. Goldfish.

Range: Native to eastern Asia, widely introduced in America as an aquarium fish and now occurs in several waters of the northeastern states and southern Ontario; in weedy areas of warm lakes and streams.

The occurrence of goldfish in lakes Erie and Ontario appears to be due chiefly to their escape from private ponds. No definite statement of introduction has been found as yet.

Cyprinus carpio. Carp.

Range: Native to central Asia, introduced widely as a food fish in Europe and America, and now common in eastern North America; in warm, preferably weedy, rivers and lakes.

The following quotation from Bensley (1915) outlines the introduction of the carp in Ontario waters:

"Regarding the introduction of this fish into Georgian Bay waters, the general opinion is that the carp of Matchedash Bay gained access to this water through the Severn River. They are reported to have ap-

peared in numbers about twelve years ago, at which time the fish were all small specimens of about 10 inches in length. Carp inhabit the head waters of the Severn River, Lake Simcoe, in large numbers, and the stock of this lake is thought to have been derived from specimens formerly kept in a pond near Newmarket. From this pond specimens are supposed to have escaped into the Holland River and thence into Lake Simcoe. It will be remembered, however, that the carp has had abundant opportunities to become distributed throughout the Great Lakes, and possibly those of Georgian Bay gained access to the waters from another direction.

"In the years from 1875 to 1879, the United States Fish Commission made several importations of German carp, with the object of stocking American waters with a type of fish that would thrive in waters unsuitable for other fishes and provide an abundant cheap food supply for the masses of the people. The carp were successfully bred, and were distributed in large numbers in successive years from 1880 to 1896. Between the years 1880 and 1893, several lots of carp were sent to applicants in Canada, including Mr. Samuel Wilmot, the Ontario Commission and certain private individuals. In Ontario the fish appear to have gained access to public waters chiefly through accidents to private ponds in which they were kept."

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SUMMARY

1. The extent of the area occupied by living forms is the resultant of two primary forces—geological and ecological.

2. Since the final retreat of the glacier some 20,000 to 35,000 years ago, Ontario has been repopulated by plants and animals which survived the ice age in areas not affected by the glaciation. This post-glacial redistribution has been influenced by the nature of the ice withdrawal and its effect on the topography of the landscape.

3. The geological history of the Ontario drainage systems as presented here has been compiled from the work of several authors.

4. Before the onset of the ice age, the region now occupied by the St. Lawrence River and the Great Lakes was drained by the Laurentian River.

5. At the maximum extent of the glacial mass most of the northern half of the North American continent, with the exception of an area in Alaska and the Yukon, was covered by ice.

6. It is believed that there were several inter-glacial periods before the final retreat of the ice cap.

7. The northeastward retreat of the glacier, the ponding and draining of the water produced by the melting ice and the elevation of the north-eastern part of the continent as the weight of ice was removed, produced a series of changes in the drainage systems of Ontario.

8. The significance of these changes lies in the opening of numerous channels through which aquatic forms could distribute themselves into the waters of the areas exposed by the retreating ice.

9. The most important of these waterways may be listed as follows:

a. Lake Agassiz—connected the Hudson Bay drainage with the Mississippi Valley;

b. St. Croix outlet from the Lake Superior basin to the Mississippi Valley;

c. Chicago outlet from the Lake Michigan basin to the Mississippi Valley, and the connections across Michigan between the Erie and Michigan basins;

d. Fort Wayne outlet from the Lake Erie basin to the Mississippi Valley.

e. Mohawk-Hudson outlet from the Lake Ontario basin to the Atlantic coastal plain;

f. Lake Algonquin stage of the Great Lakes with bays extending into the Hudson slope and the Lake Nipigon area;

g. Lake Objiway in the Hudson Bay drainage basin, and its possible connection with the Ottawa Valley through Lake Temiskaming;

h. The marine invasion from the Atlantic coast before the land could recover from its depression by the glacier.

10. The effects of the retreat of the glacier on the drainage systems, the change in climate, the nature of the land areas exposed and the physiographic changes in them since their exposure have worked in conjunction with the plants and animals available for redistribution to provide a great variety of habitats and thus to produce the present distribution of fishes.

11. There appear to have been three centres of post-glacial dispersal

in the areas not covered by the ice from which the species of fishes now occurring in Ontario have been derived: the Atlantic coastal plain, the Mississippi Valley and the Alaska-Yukon area.

12. It has been found that for the most part, the species of Ontario fishes may be placed in groups depending on the nature of their occurrence in Ontario waters. Several of these groups as well as some individual distributional problems are discussed in the present work as shown by the following outline.

a. Species of general distribution in Ontario. Several species of this group appear to have been derived from the Alaska-Yukon area, the remainder from either or both the Mississippi Valley and the Atlantic coastal plain.

b. The apparent absence of some species from the Lake of the Woods region while present in all the other chief watersheds of Ontario may be due to our incomplete information or to some undetermined geological factor.

c. Species restricted in Ontario to the waters of the southwestern tip of the province. The restriction of a number of species derived only from the Mississippi Valley to a part of Ontario with a distinctly warm climate when no apparent geological barriers present further dispersal leads to a search for an ecological barrier. Correlation of the northern limits of many of these types with the position of the 70° isotherm for July, not only in Ontario but in areas east and west of the province resulted in the conclusion that further northern dispersal of these fish has been prevented by the requirement of a certain maximum summer temperature, possibly for breeding purposes.

d. The northern limits of range of species whose Ontario occurrence extends somewhat beyond that of the previous group also show some relation to the trend of the 70° July isotherm.

e. Ecological factors appear to have been the chief barriers in restricting the dispersal of several species to southern Ontario, although geological barriers may have been effective in the case of more widely ranging species.

f. Although our information is still incomplete, the occurrence of several species in the Lake of the Woods area as well as the southern part of southern Ontario may be the result of an earlier post-glacial period warmer than the present, which allowed certain species to penetrate farther north and in some cases to adapt themselves so as to survive in spite of a return to cooler conditions.

g. The apparent correlation of the northern limits of another group

of fishes with the position of the 65° isotherm in Ontario lends support to the theory of dispersal limitations by temperature.

h. Three species occurring in southeastern Ontario have been derived only from the Atlantic coastal plain. Of these, *Leucosomus corporalis*, in extending its range to the James Bay watershed, appears to have made use of a water connection across the height of land northwest of Lake St. John in Quebec.

i. Species which present individual distributional problems.

I. It is not certain whether canals together with a tendency to range widely in all available bodies of water have been responsible for the distribution of *Polyodon spathula* in the Great Lakes.

II. The apparent separation of the occurrence of *Amphiodon alosoides* and *Hiodon tergisus* in Ontario appears to be due to competition rather than to preference of a particular habitat.

III. The occurrence of *Amphiodon alosoides* and *Imostoma shumardi* in both the Lake Winnipeg and Hudson Bay drainages indicates a water connection by which species from the western waters could pass into those of the northeastern part of Ontario.

IV. It is difficult to say whether the sole record of *Salvelinus timagamiensis* is the result of mutation or of variation under certain conditions of environment of members of a population of *Salvelinus fontinalis*.

V. *Carpiodes cyprinus*, previously believed to have come into Ontario from only the Mississippi centre, was recently found to have some Atlantic coast derivatives in the Ottawa system.

VI. *Clinostomus elongatus* appears able to live only in clear cool streams, which accounts for its localized occurrence throughout its range as well as in Ontario.

VII. *Triglopsis thompsonii*, whose nearest relatives occur in Arctic waters, is believed to have been able to survive the ice age in the cold waters at the foot of the glacier and on the retreat of the ice cap to have remained in the Great Lakes area, where deep water lakes provide the only suitable habitat.

j. Species whose distribution is discussed in relation to subspecies. The distribution in Ontario of subspecies of *Hybognathus nuchalis* and *Notropis cornutus* afford further evidence of an Atlantic as well as a Mississippi centre of redispersal.

The subspecies of *Esox masquinongy* and *Boleosoma nigrum* illustrate possible redispersal from the "driftless area" in Wisconsin as well as from the Mississippi and Atlantic centres.

k. A number of species occurring in the waters of southeastern Ontario appear to owe their presence in this region to the marine invasion.

l. A number of species have been introduced into Ontario waters as game or food fishes with varying degrees of success.

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